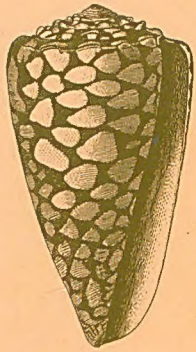

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CONTENTS

A.V. Korniushin & N. Glushchenko
Anatomy of New Zealand species of the family Sphaeriidae (Bivalvia, Eulamellibranchia) 1

B. J. Kefford & P. S. Lake
Effects of spatial and temporal changes in water velocity on the density of the freshwater snail *Potamopyrgus antipodarum* (Gray) 11

W. F. Ponder
Calopia (Calopiidae), a new genus and family of estuarine gastropods (Caenogastropoda: Rissooidea) from Australia 17

I.T. Hyman
A comparison of two onchidiid species (Mollusca, Pulmonata) 61

K.L. Lamprell & J.M. Healy
Granicorium from Australian waters, with descriptions of a new species (Mollusca: Bivalvia: Veneridae).....73

H. Wägele, G.D. Brodie & A. Klussmann-Kolb
Histological investigations on *Dendrodoris nigra* (Stimpson, 1855) (Gastropoda, Nudibranchia, Dendrodorididae).....79

Book Review
R. Willan
A revision of the Scaphopoda from Australian waters by K.L. Lamprell & J.M. Healy.....95

David G. Reid
Indo-West Pacific Ranellidae, Bursidae and Personidae (Mollusca:Gastropoda). A monograph of the New Caledonian fauna and revisions of related taxa by A.G. Beu 98

Anatomy of New Zealand species of the family Sphaeriidae (Bivalvia, Eulamellibranchia)

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Abstract

Mantle edge, gills, brood pouches and nephridia are described in *Musculium novaezelandiae* (Deshayes 1854), *Pisidium hodgkini* (Suter, 1905) and *P. novaezelandiae* Prime, 1862. Affinity of the first species to the subgenus *Sphaerinova* Iredale and placement of the second one in the subgenus *Afropisidium* Kuiper is confirmed by anatomical characters. The problem of identity of *P. novaezelandiae* and *P. casertanum* (Poli, 1791) is discussed.

Key words: Sphaeriidae, New Zealand

Introduction

Small freshwater bivalves of the family Sphaeriidae are known from New Zealand since Deshayes (1854). Four endemic species were distinguished in earlier reviews (Suter, 1913; Powell, 1957): *Sphaerium novaezelandiae* Deshayes 1854, *Pisidium novaezelandiae* Prime, 1862, *P. aucklandicum* (Suter, 1913) and *Pisidium hodgkini* (Suter, 1905). Kuiper (1966) placed the *Sphaerium* species in the subgenus *Sphaerinova* Iredale, 1943 and *P. hodgkini* in the subgenus *Afropisidium* Kuiper, 1962. He also synonymized the two remaining species with *P. casertanum* (Poli, 1791) considered a cosmopolitan species. *S. novaezelandiae* was transferred to the genus *Musculium* by Heard (1977). As considered now, the New Zealand fauna of sphaeriids consists of three species - one of the genus *Musculium* and two of *Pisidium*.

Until now only the shell characters of New Zealand species are known. However, significance of anatomical characters was shown by Odhner (1929) and confirmed by recent investigations in the Palaearctic region (Korniushin, 1992) and Africa (Korniushin, 1995). In the light of these data, anatomical investigation of sphaeriids is rather important for better understanding of their taxonomic affinities and improving classification.

In 1996, I had an opportunity to study some museum collections of New Zealand sphaeriids representing all three species known from this region. This investigation allowed to check anatomical characters of these species and provides some data on their affinities.

Material and Methods

Specimens for dissection were obtained from the Australian Museum, Sydney (AMS) (seven lots, all collected by Winston F. Ponder) and National Museum of New Zealand, Wellington (NMNZ) (three lots of different collectors). Collection details are provided with the respective descriptions.

Gross anatomy and nephridium characters were studied under the dissecting microscope, then mantle edge and gills were extracted, stained by

aqueous eosine and Grenacher`s carmine, respectively, and embedded in Canada balsam. Arrangement of ctenidium filaments and mantle muscles was studied in these slides. All drawings were made with camera lucida.

Results

Musculium novaezelandiae (Deshayes, 1854)
(Figs. 1-2)

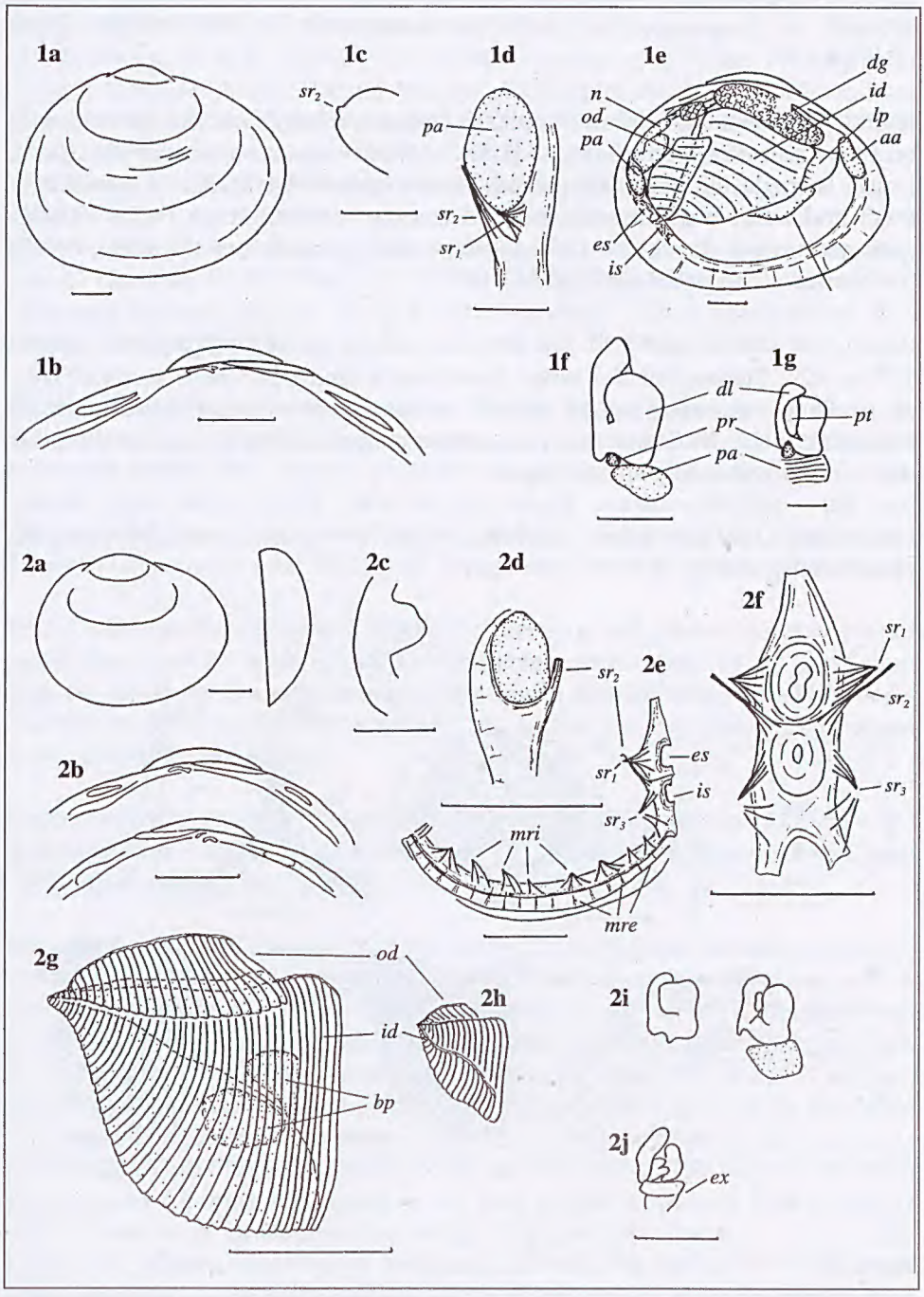
Material: Backwaters of Cluth River at Lowburn, coll. by J.R.Greenfield 30 February 1967, M131677 (NMNZ). Goulter River west of Mt.Patriarch, south of Nelson, 41°36'S, 173°9'E, in pools and small streams, collected 10 December 1982 by Winston F. Ponder, C317034 (AMS).

Mantle: Two tubular siphons. Exhalant (upper) siphon with one pair of retractors. Inhalant (lower) siphon with two pairs of muscles (Fig. 2f); upper retractors short and thin, tightly adjoining posterior adductor muscles (Fig. 1d, 2d), their scars not separated (Fig. 1c). Mantle edge rather thick and broad, both inner and outer radial mantle muscles well developed. Inner radial muscles arranged in seven bundles evenly distributed along mantle edge, four anterior bundles being strongest (Fig. 2e).

Gills: Outer demibranch present but rather small (height about 1/3 inner demibranch height), with two lamellae (Fig. 2g). In young specimens, outer demibranch begins at fifth filament of inner one (Fig. 2h). Free embryos and two brood pouches, each composed of two or three filaments, present in each gill; from 2 to 13 embryos per pouch found.

Nephridium: Both closed (with pericardial part not visible from outside) and open nephridia observed (Fig. 1f, 1g, 2i), open type more frequent in studied material. Dorsal lobe relatively broad. Excretory sac small, without internal valve (Fig. 2j); funnel long and narrow.

Figures 1 - 2. (see page facing)
Musculium novaezelandiae (Deshayes). **1.** Cluth River at Lowburn, NMNZ: **a** - right valve from outside, **b** - hinge of this valve, **c** - posterior muscle scars, **d** - siphonal retractors laterally, **e** - gross anatomy, **f,g** - nephridia dorsally; **2.** Goulter River, AMS: **a** - right valve from outside and posterior end, **b** - hinge, **c** - posterior muscle scars, **d** - siphonal retractors laterally, **e** - musculature of the mantle edge, **f** - siphonal retractors from the inner side, **g** - ctenidium of adult specimen from outside, **h** - ctenidium of the young specimen from inside, **i** - nephridia dorsally, **j** - nephridium ventrally; **aa** - anterior adductor, **bp** - brood pouch, **dg** - digestive gland, **dl** - dorsal lobe of nephridium, **es** - exhalant siphon, **ex** - excretory sac, **f** - foot, **id** - inner demibranch of ctenidium, **is** - inhalant siphon, **ll** - lateral loop of nephridium, **lp** - labial palps, **n** - nephridium, **od** - outer demibranch of ctenidium, **mri** - interior radial mantle muscles, **mre** - exterrior radial mantle muscles, **pa** - posterior adductor, **pr** - pedal retractor, **sr1** - retractors of the exhalant siphon, **sr2** - upper retractors of the inhalant siphon or their scars, **sr3** - lower retractors of the inhalant siphon. Scale bar=1 mm.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Pisidium novaezelandiae Prime, 1862.
(Fig. 3)

Material: Approximately 10 km SE of Te Aroha, north-east of Hamilton, 37°38'S, 175°40'E, in seepage, collected 31 December 1982 by W.F. Ponder (AMS C317028).

Mantle: Only exhalant siphon tubular, inhalant one being simple opening with only one pair of retractors (Fig. 3d). Pre-siphonal suture somewhat elongated, length 1/5 pedal slit length (Fig. 3d,e). Mantle edge rather thick and broad, both inner and outer radial mantle muscles well developed. Inner radial muscles arranged in six to seven rather strong and concentrated bundles evenly distributed along pedal slit (Fig. 3d).

Gills: Outer demibranch with one lamella, with its anterior edge placed against 11th or 12th filament of the inner demibranch (four specimens studied) (Fig. 3f, g). Only one brood pouch formed in lower part of inner demibranch by 5 filaments (Fig. 3f). The studied specimens contained small pouches, therefore it was not possible to count embryos.

Nephridium: Only closed type observed. Dorsal lobe square, completely covering pericardial part (Fig. 3h).

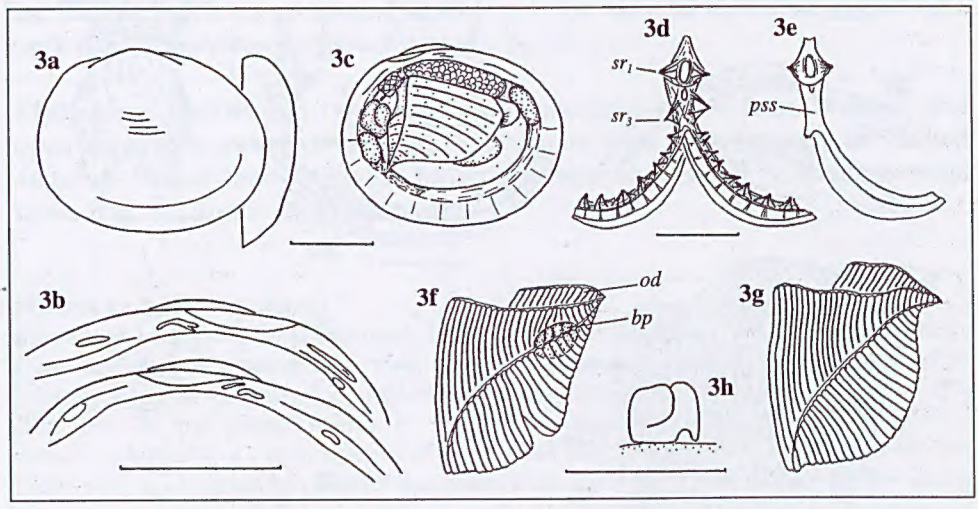


Figure 3.
Pisidium novaezelandium Prime, near Te Aroha, AMS: **a** - right valve from outside and posterior end, **b** - hinge, **c** - gross anatomy, **d** - musculature of the mantle edge, **e** - mantle edge of the other specimen, **f,g** - ctenidia from inside, **h** - nephridium dorsally; **pss** - presiphonal suture, other abbreviations as in the Figs.1-2. Scale bar=1 mm.

Pisidium hodgkini (Suter, 1905)
(Fig.4-7)

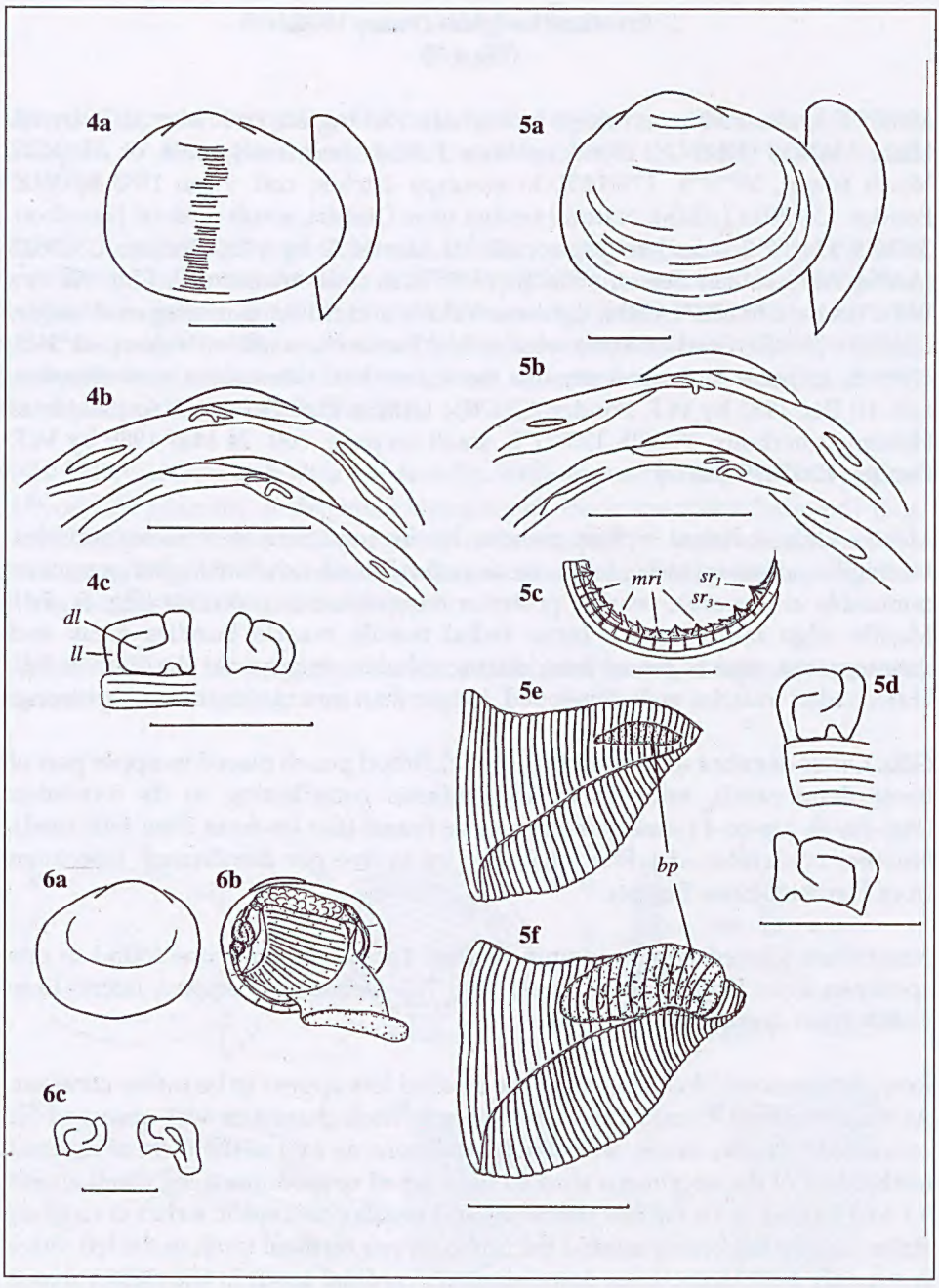
Material: Makara stream, bridge by turnoff, Wellington, coll. May 1976 by M. Hine, M47438 (NMNZ); Herekino State Forest, main road south of Ahipora, North Island, 35°13'S 173°12'E, in swampy ditches, coll. 9 Jan 1983 by W.F. Ponder, C317024 (AMS); Natural bridge near Diripiri, south-west of Hamilton, 38°13'S 174°52'E, small seepages, coll. 21 Dec 1982 by W.F. Ponder, C317025 (AMS); Waipoa State Forest, 35°57'S 173°35'E, in small trickle, coll. 7 Jan 1983 by W.F. Ponder, C317027 (AMS); the same locality and collector, in long road trickle, C317031 (AMS); Goulter River west of Mt. Patriarch, south of Nelson, 41°36'S, 173°9'E, in pools and small streams associated with *Musculium novaezelandiae*, coll. 10 Dec 1982 by W.F. Ponder, C317034 (AMS); Pine Hill road, south side of Hokianga harbour, 35°33'S 173°27'E, small seepage, coll. 24 Mar 1989 by W.F. Ponder, C317035 (AMS).

Mantle: Only exhalant siphon present, having one pair of retractor muscles. Intersiphonal suture rather long, weak rudiments of exhalant siphon retractors noticeable in this area, nearby posterior termination of pedal slit (Fig. 5c, 7d). Mantle edge rather broad. Inner radial mantle muscle bundles weak and disintegrated, nine to ten of them distinguishable along pedal slit (Fig. 5c, 7d). Outer radial muscles well developed, longer than inner ones and rather strong.

Gills: Outer demibranch absent (Fig.6b, 7c). Brood pouch placed in upper part of inner demibranch, with 13 to 18 filaments contributing to its formation (Fig. 5e, f). Up to 14 embryos per pouch found (the lot from Pine Hill road). Number of developed larvae smaller - up to five per demibranch (specimen from Herekino State Forest).

Nephridium: Closed type predominant (Fig. 4c, 5d, 7f); open one found in one specimen from Waipoa State Forest (Fig. 7e). Dorsal lobe square, lateral loop visible from dorsal side.

Remarks: Anatomical characters of the studied lots appear to be rather constant. At the same time, considerable variability in shell characters was observed. It concerns shell size, shape, and surface sculpture, as well as the form of cardinal teeth. Most of the specimens studied were small or medium sized (shell length 3.1 to 3.6 mm), with narrow umbones and regular concentric striation (coarser striae usually noticeable around the umbo); inner cardinal tooth in the left valve is strongly bent (sometimes dome-shaped), cardinal tooth in the right valve is deeply cleft, with diverging branches (Fig. 4a, b; 5a, b; 6a). The larger form (shell length up to 5.2 mm) was found in the road trickle in Waipoa State Forest. It differed also in its broader umbo, weak sculpture (only the striae around the umbo were present) and slightly bent cardinal teeth (Fig. 7a,b). It is notable, that these characters were not pronounced in the specimens from another habitat (small trickle) in the same locality, probably because of their younger age.



Figures 4 - 6.
Pisidium hodgkini (Suter). **4.** Herekino State Forest, AMS: **a** - right valve from outside and posterior end, **b** - hinge, **c** - nephridia dorsally; **5.** Pine Hill road, AMS: **a** - right valve from outside and posterior end, **b** - hinge, **c** - musculature of the mantle edge, **d** - nephridia dorsally, **e,f** - ctenidia from inside (with the subsequent stages of brood pouch development); **6.** Wellington, NMNZ: **a** - left valve from outside, **b** - gross anatomy, **c** - nephridia dorsally; abbreviations as in the Figs.1-2. Scale bar=1 mm.

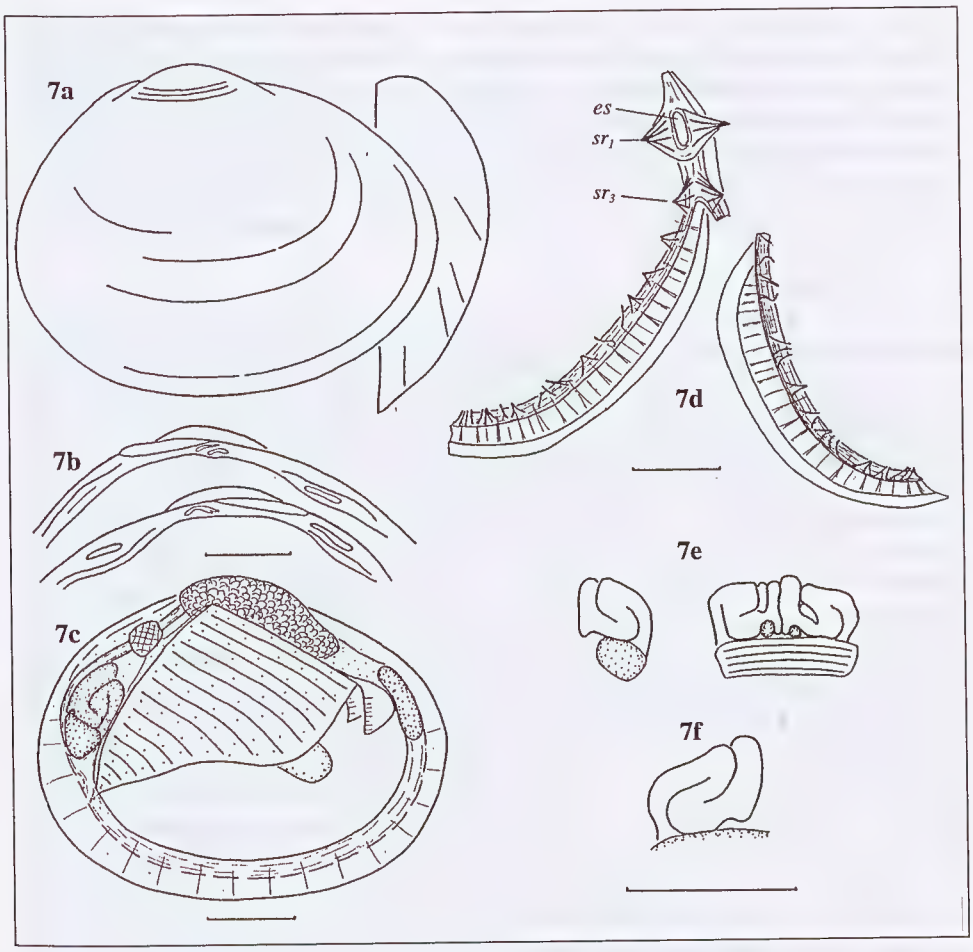


Figure 7.
Pisidium hodgkini, large form, Waipoa State Forest, AMS: **a** - right valve from outside and posterior end, **b** - hinge, **c** - gross anatomy, **d** - musculature of the mantle edge, **e,f** - nephridia dorsally; abbreviations as in the Figs.1-2. Scale bar=1 mm.

Discussion

Anatomical data provided here are rather important for defining generic and subgeneric status of New Zealand sphaeriids. Good generic characters of *Musculium*, namely relatively small excretory sac without internal valve and long funnel of nephridium, were provided by Mansur and Meier-Brook (1992). These characters were also observed in *Musculium novaezelandiae*, confirming its generic placement. As shown by Korniushin (1995), the type species of *Sphaerinova*, *Musculium tasmanicum* (Tenison Woods 1870), is characterized by rather small and weak upper retractors of the inhalant siphons. This state is supposed to be an apomorphy, while it is not found in *Sphaerium*, which may serve a suitable outgroup for *Musculium* (Mansur & Meier-Brook, 1992). In New Zealand species, reduction of siphonal muscles is even more pronounced and thus its close affinity to the Australian *Sphaerinova* is quite probable. As shown

by Korniushin (1995, 1998a), this character is also shared by a South African and several South American species of *Musculium*, thus we have a group of similar species distributed on different continents. Monophyly of the group might be supposed, but the evidence for it (weak siphonal retractors) is not sufficient. One cannot exclude that similar reduction of siphonal musculature took place independently in different clades. Therefore, decisions on species composition of *Sphaerinova* and subgeneric belonging of the New Zealand *Musculium* are not provided here.

The grounds for synonymization of *Pisidium novaezelandiae* with *P. casertanum* (Kuiper, 1966) seem to be insufficient. The New Zealand species is nearer in many characters to *P. tasmanicum* Tenison Woods, 1876, which is now considered a distinct species (Kuiper, 1983), than to European *P. casertanum*. The following characters are observed in the specimens available for this study (Fig.3a, b), in specimens from New Zealand figured by Kuiper (1966), and in *P. tasmanicum* figured by Kuiper (1983): rounded shell outline, slight posterior shift of the umbones, relatively short and almost straight dorsal margin, symmetrically placed anterior and posterior lateral teeth. At the same time, the shell of *P. novaezelandiae* is not as convex as that of *P. tasmanicum*, and the umbones are not protruding. Elongation of the presiphonal slit noticeable in the studied New Zealand specimens is another distinctive feature. However, material available for anatomical study is rather scarce and variability of the soft body structure remains unknown. In the typical Eurasian *P. casertanum*, the shell shape is nearly triangular, umbones are strongly shifted posteriorly, hinge plate strongly arched, posterior lateral teeth shorter than anterior ones and presiphonal suture short (Korniushin, 1996). Thus, there are some arguments in favour of species distinctness of *P. novaezelandiae*.

Placement of *P. hodgkini* in the subgenus *Afropisidium* is confirmed. The following significant anatomical characters observed in this species were reported for its consubgeners: absence of the outer demibranch and exhalant siphon (Kuiper, 1962), upper position of the brood pouch, especially on the early stages of its development (Meier-Brook, 1970), dorsally visible lateral loop of nephridium (Korniushin, 1992). Presence of the exhalant siphon retractors in the posterior section of the pedal slit indicates that the latter was merged to the exhalant mantle opening due to reduction of the presiphonal suture, as suggested by Korniushin (1996). Profound weakening of the inner radial mantle muscles distinguishes New Zealand *Afropisidium* from the type species *P. pirothi* Jickely, 1881, the latter species having rather strong bundles of inner radial muscles along the mantle edge (Korniushin,1998b).

Variability of the shell characters observed in *P. hodgkini* is remarkable. Specimens observed here differ from those described by Kuiper (1966) in their more pronounced sculpture and strongly bent cardinal teeth. The peculiar form found in Waipoa State Forest is larger than the forms described earlier : Kuiper (1966) reported the maximum shell length 4.5 mm. Unfortunately, the available material is not sufficient to trace up geographical pattern of the variability and to test its correlation with ecological factors. However, one may not exclude that more than one *Afropisidium* species currently lives in New Zealand, and the revision of this group seems to be necessary.

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Effects of spatial and temporal changes in water velocity on the density of the freshwater snail *Potamopyrgus antipodarum* (Gray)

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Abstract

The effects of spatial and temporal changes in water velocity on the introduced freshwater snail *Potamopyrgus antipodarum* (Gray) (Gastropoda: Hydrobiidae) were studied in an artificial stream and in Main Creek, Victoria, Australia. The water velocity at which *P. antipodarum* became dislodged in the artificial stream was in agreement with their distribution in Main Creek. In Main Creek the density of *P. antipodarum* on a standard substrate (half bricks) was negatively correlated with water velocity. However, no evidence was found that increases in water velocity associated with floods affect the densities of *P. antipodarum*.

Key words: water velocity, density, *Potamopyrgus antipodarum*

Introduction

Stream ecologists have long considered that the velocity of flowing water influences macroinvertebrate populations in lotic systems (Dittmar, 1955; Dorier, and Valliant, 1955; Hynes, 1970). The nature of the flow environment varies both spatially and temporally (Ward, 1992) and at many scales (Minshall, 1988). This study investigates the effect of spatial and temporal changes in water velocity on the freshwater snail *Potamopyrgus antipodarum*. Specifically, we examine whether *P. antipodarum* density is affected by spatial variation in water velocity and by floods. We hypothesise that in areas of high water velocity *P. antipodarum* is physically removed from the substratum by the force of the moving water. We test this hypothesis by a combination of field and laboratory observations.

Materials and Methods

The study was conducted in Main Creek, a small unregulated stream located approximately 80 km from Melbourne, Victoria, Australia, in a south eastern direction, at a site where it is crossed by Boneo Road (38°29'S, 144°55'E).

Velocities that dislodge P. antipodarum

Using the artificial stream described by Horne and Bennison (1987), tests were carried out to determine the velocity at which *P. antipodarum* were dislodged from the substratum. The velocity at which a snail became dislodged and entered the drift was regarded as the maximum velocity which that individual could withstand.

A single *P. antipodarum* was placed on a small patch of fine sandpaper fixed to the bottom of the channel. The sandpaper was used to provide a more 'natural' substratum than the plexiglass of the channel. Once the *P. antipodarum*

had attached to the sandpaper, the velocity was gradually increased from zero until maximum velocity was obtained or the *P. antipodarum* became dislodged. At this point the water velocity was measured with a digital Nixon flow-meter with a propeller diameter of 8 mm. Dislodged snails were caught in a net and their length, width and live mass measured. Ten replicate *P. antipodarum* were tested.

The 'riffle-scale' relationship between the density of P. antipodarum and velocity.
At the scale of a riffle, density of *P. antipodarum* on 62 half bricks and bottom velocity were related by standard correlation. The bricks were used as standard substrate to prevented observations being confounded with different substrata occurring with different water velocities.

The bricks were conditioned for algae by leaving them in Main Creek for approximately two months. The experiment would have been confounded if algae that favour specific velocities (see Power and Stewart, 1987) were present in Main Creek. To avoid this, the bricks were moved, in a haphazard manner, before the experiment so that bricks conditioned at a certain velocity were not necessarily exposed to the same velocity in the experiment. So that all bricks were independent of each other, they were at least 0.5 metres from all neighbouring bricks.

The number of *P. antipodarum* per half brick was counted in the field with the aid of a viewing box on two occasions. The water velocity was measured on top of the brick with a Marsh-McBirney magnetic flow-meter (which measures the water velocity at 1.8 cm above the substrate). The depth of the brick was measured with a ruler and the distance from the bank estimated. The amount of turbulence was visually assigned an ordinal score of 1, 2 or 3. The turbulence index, the water depth and the distance to the bank were used to take into account these potentially confounding factors in a multiple regression equation.

'Smaller-scale' relationship between the density of P. antipodarum and velocity
The relationship between water velocity and *P. antipodarum* density on the scale of an individual half brick was investigated. The numbers of *P. antipodarum* on each of the five visible sides of the 62 half bricks were counted with the aid of a viewing box and velocities on each side were measured using a Nixon flow-meter with the velocity measured closer to the substrate (0.8 cm above the substrate). The null hypothesis was that there is no relationship between the number of *P. antipodarum* per brick side and the water velocity. If correct, there would be an equal number of bricks with negative and positive correlations between density of *P. antipodarum* and velocity. For each brick it was determined whether the slope of the least squares regression line (n=5) was positive or negative and the difference in the observed and the expected relationships for all bricks was assessed in a chi squared test.

The effect of floods on P. antipodarum
The effects of floods on the density of *P. antipodarum* was investigated in September 1993 by taking 9 randomly located replicate samples per sampling episode with an electric suction sampler (Brooks, 1995) from a riffle in Main

Creek before and during three floods occurring close together. Samples were preserved and *P. antipodarum* were counted under a dissecting microscope. A pilot study suggested that 9 replicate samples would be sufficient to gain reasonable power. The null hypothesis was that the flood would have no effect on the density of *P. antipodarum*.

The flood sequence consisted of three closely spaced small floods at an increasing intensity. The 'before flood' sample was taken about 7 days before the first flood when discharge was estimated to be 0.14 $m^3.sec^{-1}$. The 1st (and smallest) flood had an estimated discharge of 0.51 $m^3.sec^{-1}$, the 2nd flood 0.59 $m^3.sec^{-1}$ and the 3rd (and largest) flood 2.1 $m^3.sec^{-1}$. In addition to the sampling before and during the floods, samples were taken after the final flood to monitor any recovery. The 'recovery' (or after) samples were collected 3, 6, and 8 days after the largest flood.

Additionally, non-destructive measurements of *P. antipodarum*, with the aid of a viewing box, on 49 half bricks were made before (day 1) and after (day 4) a separate small flood (estimated discharge 0.60 $m^3.sec^{-1}$).

Results

Dislodgment of P. antipodarum

The minimum and mean velocities at which *P. antipodarum* were dislodged in the artificial stream were 15 and 67.6 ± 8.3 $cm.sec^{-1}$, respectively. However a single *P. antipodarum* remained attached at the maximum velocity that could be produced in the artificial stream 95.4 $cm.sec^{-1}$.

There was no significant linear correlation between the velocity at which a *P. antipodarum* was dislodged and its length, width, length:width ratio or live mass and there was no obvious non-linear correlation (by inspection of scatter plots).

Correlations between water velocity and P. antipodarum density on the bricks

There were significant negative correlations between the log number of P. antipodarum per half brick and the bottom velocity (range 0 to 120 $cm.sec^{-1}$) for both days ($r=-0.431$, $P<0.001$; $r=-0.404$, $P=0.001$, respectively) (Figure 1). Using multiple regression to take into account the effect of depth, distance from the bank and turbulence, these relationships were still significant ($b_1=-0.008$, $P=0.017$; $b_1=-0.007$, $P=0.027$, respectively).

At the smaller scale of an individual side of a half brick, there were significantly more bricks observed with negative relationships than positive relationships between *P. antipodarum* density and velocity than would be expected by chance (chi sq=4.569, df=1, $P<0.01$).

The effect of floods on P. antipodarum

During the peak of the flood mean water velocity reached 94 ± 16.6 $cm.sec^{-1}$. However there was no significant difference in *P. antipodarum* density at the different sampling episodes ($F=2.013$, df= 6 & 56, $P=0.079$, $\beta = 0.307$) (Figure 2). A planned comparison showed no significant difference in the mean density between before flood and during or after the largest flood sampled ($F=1.890$, df=1 & 56, $P=0.175$).

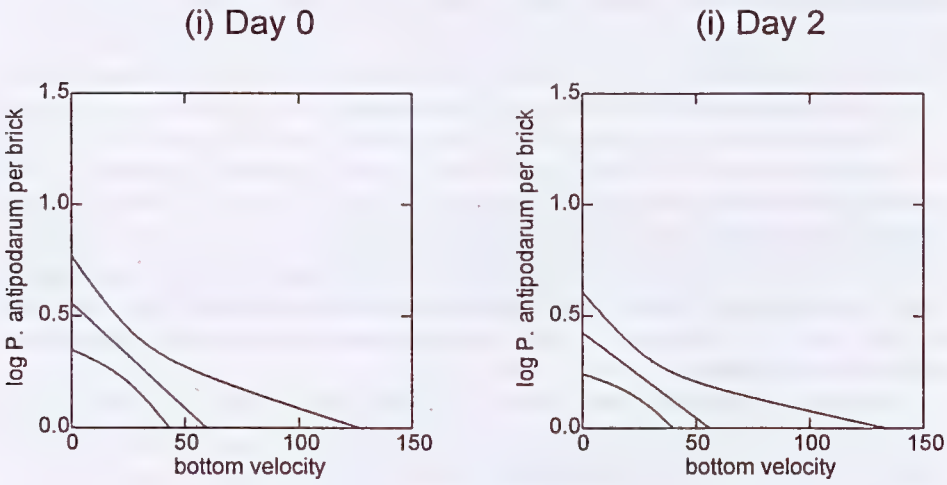

Figure 1.
Scatter plots of log *P. antipodarum* density on half bricks and bottom velocity (cm/sec) on (i) Day 0 and (ii) day 2. The lines are least square regression lines.

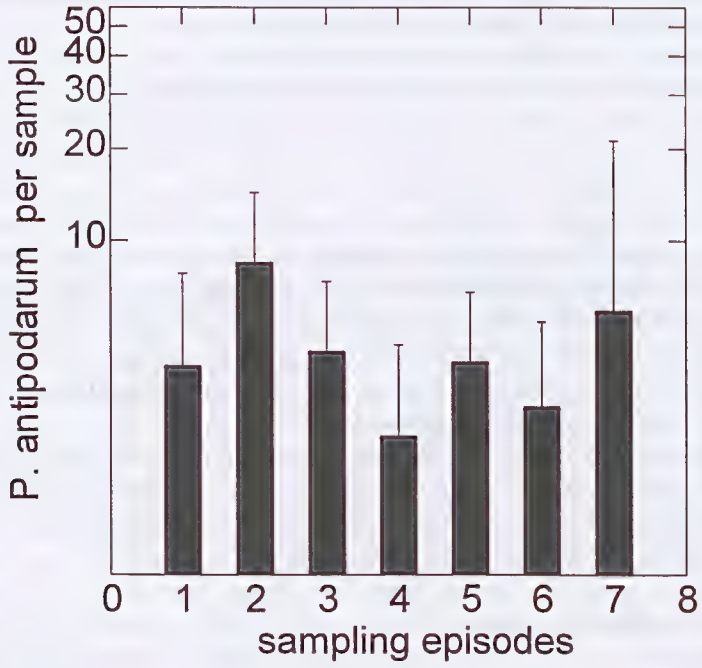

Figure 2.
The relationship between *P. antipodarum* per sample before, during and after a flood sequence, where 1= before flood, 2= during the smallest flood, 3= during the medium level flood, 4= during the larger flood, 5= day 3 after the largest flood, 6= day 6 after the largest flood and 7= day 8 after the largest flood.

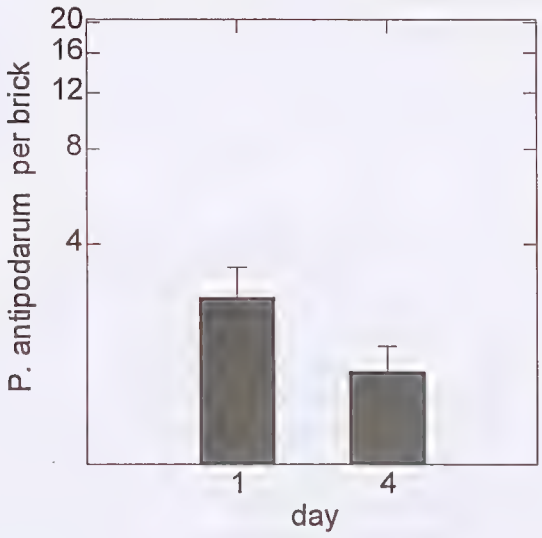

Figure 3.
P. antipodarum per visible portion of half bricks before (=1) and after (=4) a small flood. Error bars are the standard error of the mean.

Similarly, there was no significant difference in the mean log number of *P. antipodarum* per half brick between before and after the flood ($F=2.120$, $df=1$ & 42, $P=0.153$) (Figure 3).

Discussion

At both the spatial scales investigated, the effect of fast moving currents on *P. antipodarum* appeared to be similar. Density of *P. antipodarum* and bottom water velocity were negatively correlated at both the spatial scales investigated, riffle and half brick. In the artificial stream, the mean water velocity at which *P. antipodarum* was dislodged was 67.6 ± 8.3 cm.sec^{-1}. This is in broad agreement with observations in Main Creek where *P. antipodarum* was not observed on the half brick in water velocities above 50 cm.sec^{-1}. The higher value obtained in the artificial stream is probable related to *P. antipodarum* being exposure to higher water velocities for longer in Main Creek than the artificial stream (Holomuzki and Briggs, 1998).

Correlations do not imply causality due to the potential for confounding factors. Measures of water velocity are well known to be confounded by other factors (Ward, 1992). However, by using bricks some potentially confounding factors were eliminated and others were taken into account and, combined with the artificial stream result, suggest that *P. antipodarum* density is being reduced by high water velocity physically forcing them off the substrata.

Why would *P. antipodarum* densities be reduced in areas of fast flowing water while during floods, which are characterised by fast flowing water, their densities would be unaffected? The answer to this question may be that different processes are occurring between temporal and spatial changes in water velocity. If the lack of *P. antipodarum* in areas of high water velocity is caused by the force

of the current physically removing *P. antipodarum*, at first thought one would expected that temporal increases in water velocity would remove *P. antipodarum* from their substrate. However, as water velocity increases during the onset of a flood, *P. antipodarum* may be able to detect the rise in water velocity and move to refuges. This explanation is supported by Holomuzki and Birggs (1988) who found that *P. antipodarum* sought crevices during experimental increases in water velocity.

Even if *P. antipodarum* are forced off their substrate by rising water velocity during floods, it does not necessarily follow that floods will reduce the densities of *P. antipodarum* at a given site. Mortality of *P. antipodarum* dislodged from substrate has been observed to be low (2 - 5%) (Holomuzki and Biggs, 1988). So within a site, a flood may wash *P. antipodarum* downstream but live *P. antipodarum* that have themselves been washed away upstream may be deposited in eddies and backwaters at that site. The change in density of *P. antipodarum* at a site following a flood may depend on the number that are exported and the number that are imported. Thus, in a given area, a flood may result in the density of *P. antipodarum* increasing, decreasing or staying constant. This is in agreement with Holomuzki and Birggs (1988) who noted that flow disturbance seemed to affect *P. antipodarum* more by displacement than by killing them.

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Calopia (Calopiidae), a new genus and family of estuarine gastropods (Caenogastropoda: Rissooidea) from Australia

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Abstract

A new family, Calopiidae is described for a new genus and four species, three of them new, from estuarine habitats in Australia. While similar to many rissooideans in having a simple, conical shell, Calopiidae can be distinguished from all other taxa by a unique combination of apomorphic characters, including a simple operculum with calcareous-like opaque-white material on its inner surface. The long cephalic tentacles have complex ciliation, including long, distal compound cilia. The foot has an anterior cleft and the propodium lies dorsally behind the anterior edge of the foot. There is a short metapodial tentacle close to the posterior margin of the foot. The osphradium is longer than the poorly-developed ctenidium, the latter unusual in lacking skeletal rods. The intestine loops around the middle of the style sac, not at its anterior end as in most other caenogastropods, and the rectum forms a tight S-shaped coil on the pallial roof. The testis is composed of a few large, long lobes and the prostate gland is triangular and closed. The large penis has a few large apocrine glands. The female system is unusual in lacking a seminal receptacle and in the oviduct gland being uniform throughout. The spawn consists of short rows of capsules and larvae hatch as swimming veligers. The relationships of the new family are assessed following a cladistic analysis, using 49 informative morphological characters, of similar rissooidean taxa. The strict consensus of the 40 shortest trees shows *Calopia* as the sister of the four taxa in the analysis that are currently included in the Hydrobiidae. A replacement name, *Calopia laseroni*, is provided for *Lucidestea perforata* Laseron, 1956, a secondary homonym of *Lucidestea perforata* (Thiele, 1925).

Key words: *Calopia*, Calopiidae, new taxa, estuarine gastropods Australia

Introduction

Small gastropods are abundant in most shallow-water marine ecosystems throughout the world but poor taxonomic knowledge of many groups has prevented their adequate utilisation in ecological and other studies. While understanding of some of the most common groups in Australia has progressed in recent years much still remains to be done. The group described in this paper is common in estuarine ecosystems in much of eastern and northern Australia but from the south coast is known only from Victoria. Of the three species recognised herein, only one has previously been named. The group has not been positively identified outside Australia.

This new taxon is a member of the Rissooidea, one of the largest superfamilies of gastropods, which contains many groups of mainly small-sized marine taxa, as well as freshwater and terrestrial families. The simple shell morphology found in many rissooidean taxa has obscured relationships. Indeed, the small, conical, smooth shell seen in the new taxon described in this paper is similar to that seen in many species in a number of unrelated families of gastropods including Skeneidae *s.l.* (Vetigastropoda), and the caenogastropod Cingulopsidae and Eatoniellidae (Cingulopsoidea) as well as the more closely

related rissooidean families Rissoidae and Hydrobiidae. Ponder (1988) provided a cladistic analysis of the Cingulopsoidea and Rissooidea (as Truncatelloidea). A subset of the rissooidean taxa is reanalysed below in an attempt to determine the relationships of the new taxon.

Abbreviations

Repositories

AMS, Australian Museum, Sydney
LACM, Natural History Museum, Los Angles
MV, Museum of Victoria, Melbourne
MONZ, Museum of New Zealand, Wellington
NMNHP, National Natural History Museum, Paris
NTM, Northern Territory Museum, Darwin
QM, Queensland Museum, Brisbane
SAM, South Australian Museum, Adelaide
USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.
WAM, Western Australian Museum, Perth

Measurements

SL, shell length
SW, shell width
AL, aperture length
AW, aperture width
WH, total whorls

W.F. Ponder is abbreviated to initials in material examined.

Materials and Methods

Specimens of the type species of the genus were collected from Maianbar, Port Hacking, Salamander Bay, Port Stephens, and Careel Bay, Pittwater, all New South Wales, Australia. These were examined alive and fixed in Bouin's fixative or 5-10% formalin and dissected. The anatomical description is based on the type species. Bouin's fixed material was also serially sectioned in paraffin and stained with Cason's trichrome and haematoxylin and eosin. Living material of two of the other species was also examined (see descriptive section for details).

A cladistic analysis was undertaken using PAUP* (Beta test version 64). The sources for the data used for taxa other than the new genus described below, are given in the appendix. All characters were unweighted and unordered. The analysis presented is a heuristic search with 10 random iterations using the default parameters. SYSTAT ver. 5 was used for the statistical procedures.

Systematics

Calopiidae new family

The diagnosis for the new family is the same as for the genus described below. Discussion of the distinguishing features and the rationale for creating a new family, as well as its relationships, is given below under `Phylogenetic Relationships'.

Calopia new genus

Type species: Calopia imitata n.sp.
Diagnosis:
Shell: Conical to trochiform, umbilicate, smooth, with convex whorls and simple aperture. Protoconch nearly two whorls, with small spirally sculptured initial whorl but no clear division between protoconch I and II.
Operculum: Paucispiral, subcircular to oval, with calcareous-like opaque white material on inner surface of middle area.
Head-foot: Cephalic tentacles long, parallel-sided, with compound cilia distally, cilial tracts on anterior, posterior and ventral edges and low ciliated knobs on outer proximal edge of left tentacle. Left side of neck with horizontal ciliated stripe and no vertical stripe on right. Foot elongate, cleft anteriorly, with propodium on dorsal surface behind anterior edge. Anterior pedal gland present, no posterior pedal gland. Posterior foot tapering, with short metapodial tentacle close to posterior margin. Mantle edge lacking pallial tentacles.
Anatomy: Ctenidium poorly developed, with filaments lacking skeletal rods. Osphradium elongately oval, longer than ctenidium. Hypobranchial gland very thick posteriorly. Alimentary canal typical of superfamily in most characters. Central teeth with formula 2 (-3)+1+2 (-3) with 1 pair of basal denticles. Lateral teeth each with formula 2-3+1+4-6, a basal denticle and short outer wing. Inner and outer marginal teeth have several small sharp cusps about equal in size. Intestine loops around middle of style sac. Rectum forms tight S-shaped coil on pallial roof. Digestive gland lacks concretions. Testis composed of few large, long lobes. Prostate gland triangular, closed ventrally, with narrow lumen. Pallial vas deferens straight, narrow, simple. Penis large, with long, tapering distal section and short, wide basal section; junction with several (up to 8) large apocrine glands and, in some species, another glandular lobe on base. Renal oviduct very short, opens to common oviduct along with short duct from large, near globular bursa copulatrix lying immediately behind oviduct gland. Bursal lumen with both orientated and unorientated sperm, no separate seminal receptacle present. Oviduct gland, like prostate, composed of complex glandular epithelial cells and uniform throughout (no separate albumen gland present); all of pallial oviduct gland lies within pallial cavity. Ventral channel with deep sperm gutter on left, oviduct opening terminal. Nervous system typical of hydrobioid families (*sensu* Hershler & Ponder, 1998) but with unpigmented ganglia. Renal and pericardial anatomy similar to other hydrobioid taxa, with posterior renal organ and opening. Spawn consists of rows of 3-8 capsules; larvae hatch as swimming veligers.

Description (based on *C. imitata* n.sp.)
Shell: The shell (Figs 1, 11) is smooth except for a few spiral grooves on the base and is conical to trochiform in shape. The convex base is narrowly to widely umbilicate and the convex whorls are regularly increasing. The aperture has a simple, thin peristome, is angled posteriorly and rounded and simple anteriorly. The inner lip is often separated slightly from the parietal wall. The protoconch (Fig. 12) consists of about one and three quarter to nearly two whorls, with a

Figure 1.
Shells of *Calopia* species: **A-D** *Calopia imitata* n.sp., (A) Careel Bay, Pittwater NSW (C 316251), (B) Basal view, paratype, Salamander Bay, Port Stephens, NSW (C 316257), (C) Holotype, Salamander Bay, Port Stephens, NSW (C 337879), (D) S. of Urangan Boat Anchorage, Hervey Bay, QLD (C 322943). **E-F** *Calopia burni* n.sp., (E). Basal View. Jetty at Stony Pt., Westernport., VIC (C 327378); (F) Holotype, Jetty at Stony Pt., Westernport, VIC (C 337883). Scale 500 μm

small initial whorl. It is smooth except for few (about 5) very fine, slightly raised, lines (Fig. 12) that are easily worn away. There is no obvious division into protoconch I and II.

Operculum: The spiral operculum (Fig. 2) is subcircular to oval, slightly concave and the relatively large circular nucleus takes up to about two thirds of the diameter of the adult operculum. The following 2-3 whorls are tightly coiled, juveniles having a circular operculum. The last whorl expands rapidly resulting in a subcircular outline in the adult. The central two thirds of the inner side is opaque-white (this showing through to the outer side) and slightly thickened, the outer parts being thin and transparent. The thickened internal area is bordered by a raised, sharp edge behind the columellar edge of the operculum (Fig. 2A,D,F).

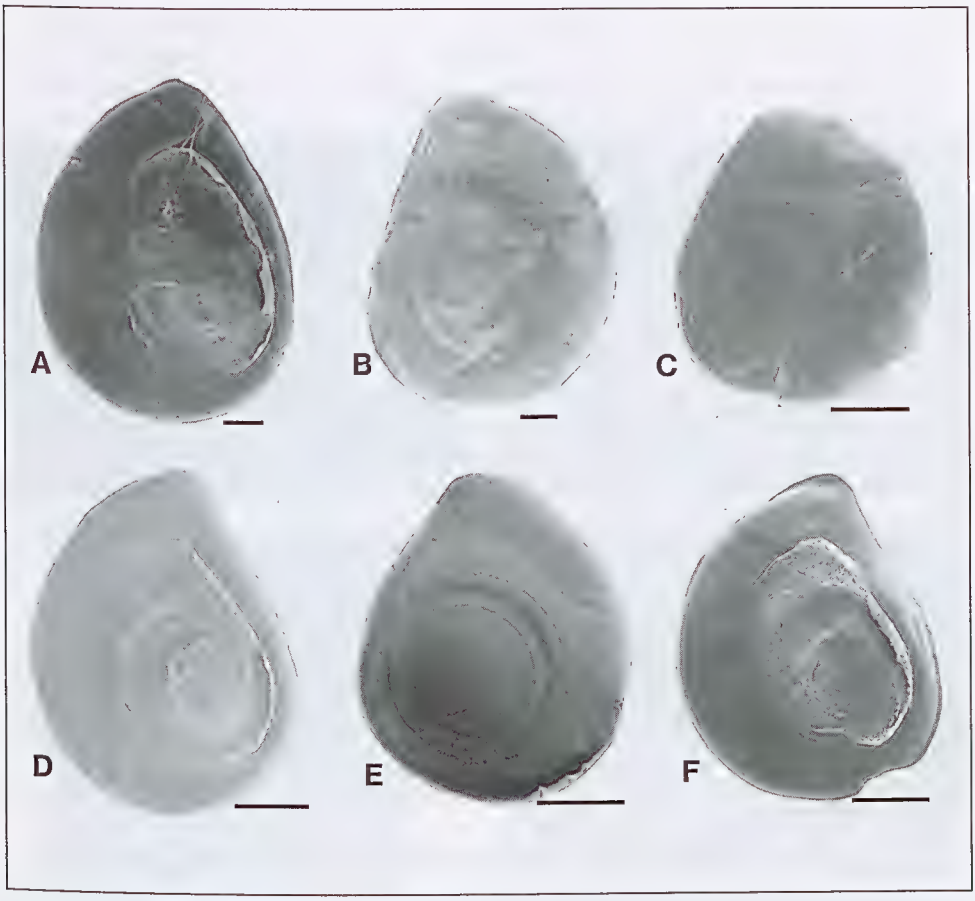

Figure 2.
Opercula of *Calopia* species: **A-B** *Calopia imitata* n.sp., (A) inner side, Salamander Bay, Port Stephens, NSW (C 316257), (B) outer side, Fishermans Bay, Port Hacking, NSW (C 338919). **C** *Calopia laseroni* n.nam., Mission Bay, Broome , WA (C 337887), outer side. **D-E** *Calopia minutissima* n.sp., Nightcliff, Darwin, NT (C 330800), (D) inner side, (E) outer side. **F** *Calopia laseroni* n.nam. Mission Bay, Broome, WA (C 337887), inner side. Scale 100 μm.

Head-foot: (see species descriptions for details of pigmentation). The head (Figs 4, 5, 8) has semitranslucent, yellowish-white cephalic tentacles that are long, parallel-sided and distally rounded and held approximately horizontally. There is a zone of black pigment a little more than half way along the tentacle from the base and, in the type species, another at the base. Distally the tentacles bear a cluster of compound cilia (Fig. 4A-D) and there are strongly beating cilial tracts on the anterior and posterior edges. Ventrally there is a ciliated tract in the proximal half and, close to the distal end, an oblique tract (Fig. 4A, **ot**). There are also two to several (usually four) low ciliated knobs on the outer proximal edge of the left tentacle, usually extending to slightly more than half the length of the tentacle (Fig. 5A, **ck**). The conspicuous eyes are in weak bulges at the outer bases of the tentacles. The snout is slightly tapering when at rest, weakly bilobed distally, and has black pigment laterally. While the snout is normally rather

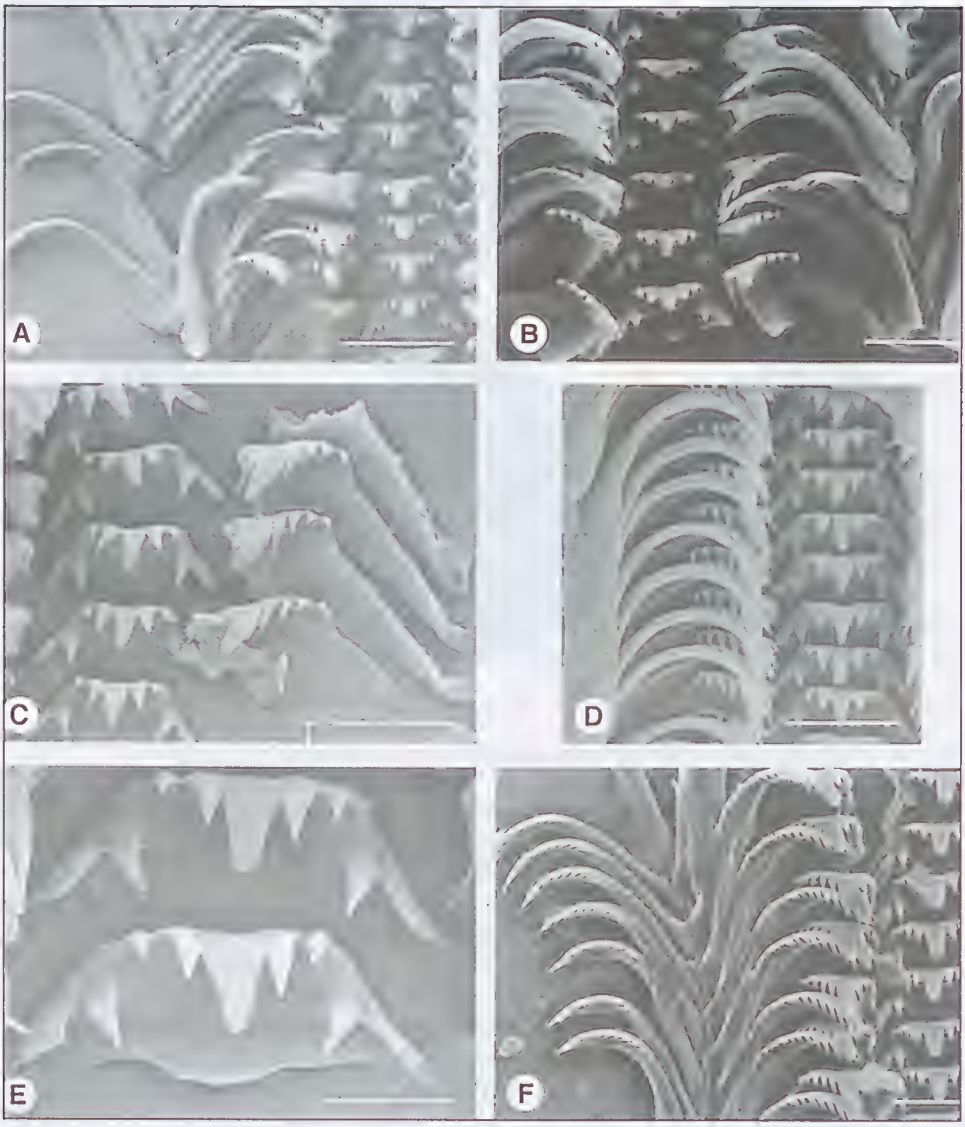

Figure 3.
Radula of *Calopia* species: **A** *Calopia imitata* n.sp.. Salamander Bay, Port Stephen, NSW. **B** *Calopia laseroni* n.nam. Mission Bay, Broome, WA. **C-E** *Calopia minutissima* n.sp. Nightcliff, Darwin, NT, (C) detail of central and lateral teeth, (E) detail of central teeth. **F** *Calopia burni* n.sp. Jetty at Stony Point, Westernport, VIC. Scales A 20 μm, B-D, F 10 μm, E 5 μm.

short, it is capable of extending to nearly double its resting length to slightly more than two thirds the length of the cephalic tentacles. When extended the snout is slightly wider distally than proximally, the yellowish-white (not pink or red as in some other rissooideans) buccal mass within it. The snout is complexly ciliated, with several largely oblique cilial tracts laterally becoming stronger and vertical latero-ventrally (Fig. 4G,H). The sides of the neck are uniformly pigmented, lacking the unpigmented ciliated vertical stripe found in most rissooideans on the right. Along the side of the `neck' on the left there is a horizontal, slightly crescent-shaped, unpigmented stripe on which cilia drive particles postero-dorsally. The narrow, elongate foot is cleft anteriorly with a broadly V-shaped dorsal ridge (the anterior edge of the propodium), usually darkly pigmented, running transversely behind the anterior edge (Fig. 5B, **pr**). The conspicuous triangular anterior pedal gland (Fig. 5B, **amg**) opens beneath the propodial rim. It consists of a series of small glands spread laterally and a large posterior, median gland. There is no posterior pedal gland apart from subepithelial mucous glands in the sole. Posteriorly the foot tapers and, dorsally, bears a short metapodial tentacle attached close to the posterior margin (Figs 4E, 5, **mt**). The mantle edge (Fig. 4F) is ciliated, especially at the posterior corner with the cilia carrying particles and faecal pellets to the exterior. A darkly pigmented, densely ciliated flap of tissue formed from the outer mantle lobe (Fig. 4F, **oml**) lies in the posterior (right) corner of the aperture with the inner mantle lobe (Fig. 4F, **iml**) raised above this, forming a distinctly separate, thin, inner rim. The two mantle lobes are not noticeably separated around the rest of the aperture. Movement is by rather rapid ciliary gliding.

Pallial cavity: The ctenidium (Fig. 6A, **ct**) is poorly developed, with about 11-13 short triangular filaments lacking skeletal rods. The filaments commence a little behind the anterior edge of the pallial cavity and terminate just short of the auricle to which they are connected by a well-developed efferent branchial vein (Fig. 6A, **ebv**). The large, elongately oval osphradium (Fig 6A, **os**) has a low central sensory area which is surrounded by broad (about as wide as the central area) ciliated ridges that provide a strong inwardly directed current. The osphradium extends from the posterior end of the pallial cavity almost to the anterior pallial edge and is thus longer than the ctenidium, extending further both posteriorly and anteriorly. Posteriorly, the mantle cavity is almost filled with a very thick, almost circular pad (Fig. 6A, **hg**), a part of the hypobranchial gland, that stains bright red in Cason's trichrome and, on fixation in Bouin's fixative is dark wine-red. This section of the hypobranchial gland is firmly attached to the posterior part of the glandular gonoduct and an anterior loop of the rectum extends anteriorly from this pad to about the anterior third of the ctenidium, between the ctenidium and the rectum + gonoduct. The remainder of the hypobranchial gland is relatively inconspicuous.

Alimentary canal: The small, paired jaws are composed of a few stout rodlets and lie anterior to the well-developed odontophore. The simple, short, tubular salivary glands extend dorsally over the nerve ring. The radular sac does not extend behind the buccal mass and the radula (Fig. 3) is taenioglossate. The

central teeth have a straight cutting edge with 2 (rarely 3) short, pointed cusps on either side of the large, typically blunt median cusp. A single, prominent basal denticle lies just inside each thickened lateral margin, the latter at about 40° to the vertical axis. These margins extend only slightly beyond the straight base that has only a very weak basal tongue present. The lateral teeth have a typically blunt primary cusp, several (4-6) very small cusps on the outer side and 2-3 cusps on the inner side. There is a prominent basal denticle and the outer wing is short, about 1.4-1.9 times the length of the cutting edge. The inner marginal teeth have several (10?-18) sharp cusps on their outer edges and the outer marginal teeth have several (>7) sharp cusps on their inner side. The anterior and mid-oesophagus contain a pair of long, straight dorsal folds and, ventrally, the epithelium contains some small glandular (mucous?) cells. The posterior oesophagus is a simple, narrow tube. The moderately large, mainly black-pigmented stomach (Fig. 6E) contains amorphous detritus, minute particles, diatoms and other single-celled organisms. There is a single digestive gland opening (**dgo**) and no posterior caecum. The style sac (**ss**) is about the same length as the stomach proper and contains a crystalline style. The intestine (**int**) opens to the stomach and is separated from the style sac. The proximal intestine has a broad typhlosole occupying much of the lumen and this section contains unconsolidated faecal material. This part of the intestine is unusual in that it loops around the middle of the style sac (not the anterior end as in most other rissooideans and in most other caenogastropods). The free anterior end of the style sac is narrower anteriorly than posteriorly, giving it a somewhat pointed appearance. The rectum forms a tight S-shaped coil in the pallial roof (seen in all the species of *Calopia*). The proximal loop is typically packed with oval pellets but the terminal arm is often empty. The anus lies close to the mantle edge on the right side of the pallial cavity and forms a short papilla. The digestive gland, together with the gonad, occupies the visceral coil behind the stomach and an anterior lobe consisting of a single, initially broad, tubule extends anteriorly to lie beneath the posterior part of the style sac. There appears to be only a single type of digestive cell and there are secretory cells lying at the bases of folds in the lumen. Excretory cells with concretions are absent.

Reproductive system: Male: The testis (Fig. 6D, **t**) is composed of a few large, long lobes through most of the visceral coil behind the stomach and two lobes that extend over the stomach. The rope-like seminal vesicle (Fig. 6D, **sv**) runs back about half the length of the testis and then loops forward to join the narrow vas efferens. The short prostate gland lies in the posterior end of the pallial cavity, its wide posterior edge abutting against the kidney. It is approximately an equilateral triangle, has a narrow lumen, its thick walls having a complex histology (Ponder, 1988) and there is no external opening, The conspicuous, thin-walled pallial vas deferens (Fig. 10A, **vd**) runs straight from the postero-ventral edge of the prostate gland to the base of the penis. The large penis (Figs 4H, 8, 10) lies just to the right of the midline well behind the bases of the tentacles. It consists of a long, narrow, tapering distal section and a short, wide basal part (Fig. 10A, **pb**). Projecting from the junction of the basal and distal parts of the penis are several (up to 8, but only 2 in one species) large apocrine

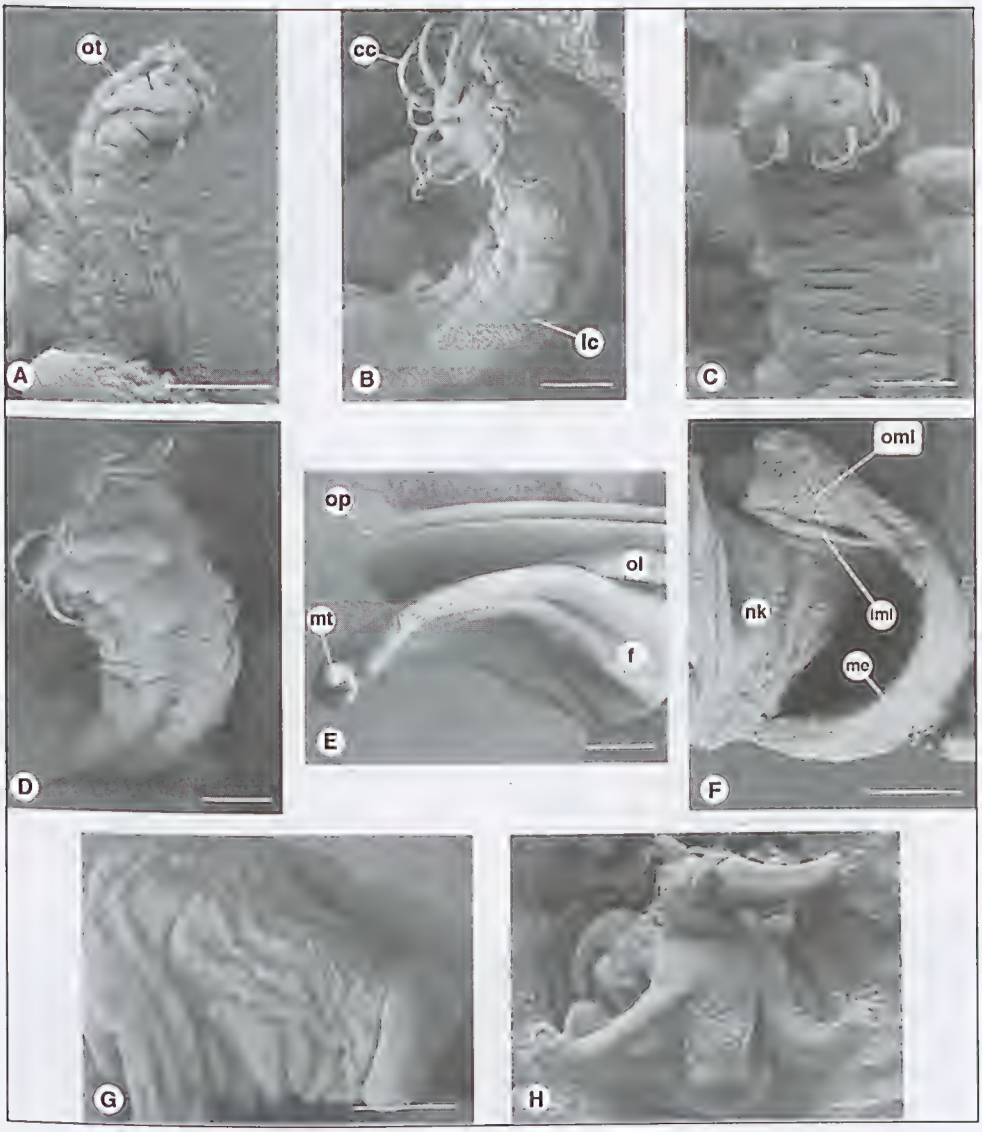

Figure 4.
A-H Head-foot and penis of *Calopia imitata* n.sp., Salamander Bay, Port Stephens, NSW, (A) Ventral view of right cephalic tentacle showing lateral bands of cilia and ventral cilia. (B) Inner lateral view of left cephalic tentacle showing lateral and dorsal bands of cilia and distal compound cilia. (C) Distal tip and dorsal surface, left cephalic tentacle showing cilial bands and detail of distal compound cilia. (D) Head, ventral view, left cephalic tentacle showing detail of distal diagonal band of cilia, longitudinal cilial bands and distal compound cilia. (E) Lateral view of right side of posterior end of foot and operculum. (F) Mantle edge showing broad ciliated area of mantle edge at right side of aperture and cilia on neck region. (G) Right dorso-lateral view of snout showing complex cilial tracts. (H) Dorsal view of head and penis. **cc** - compound cilia, **f** - foot, **iml** - inner mantle lobe, **lc** - lateral cilial band, **me** - mantle edge, **mt** - metapodial tentacle, **nk** - neck, **ol** - opercular lobe, **oml** - outer mantle lobe, **op** - operculum, **ot** - oblique ciliated tract. Scales A, E-H 100 μm, B-D 50 μm.

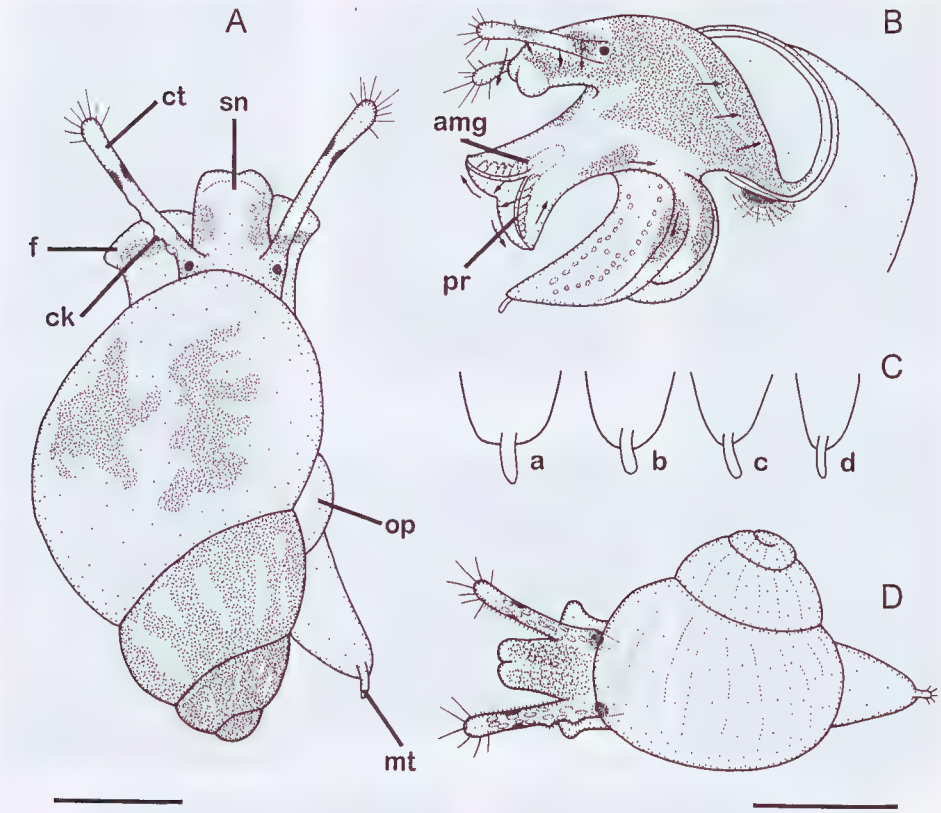

Figure 5.
Head-foot of *Calopia* species. **A-C** *Calopia imitata* n.sp. Salamander Bay, NSW. (A) Dorsal view of living animal, (B) lateral view of head and foot showing ciliation patterns and details of dorsal side of anterior foot, (C) variation in posterior end of foot. **D** *Calopia minutissima* n.sp. Dorsal view of living animal. Nightcliff, Darwin, NT. **amg** - anterior mucous gland, **ck** - ciliated knobs; **ct** - ctenidium, **f** - foot, **mt** - metapodial tentacle, **op** - operculum, **pr** - edge of propodium, **sn** - snout. Scales 0.5 mm.

glands (Figs 8, 10, **ap**). These are semi-transparent, colourless with a denser, white area at their distal end. A basal glandular lobe projects from the proximal part of the basal section of the penis (Figs 8, 10, **bl**). The penis has a thick glandular epithelium and a narrow, straight central duct (Fig. 10A, **pd**), although distally the epithelium is simple and thin and the duct very narrow. The apocrine glands have a very thick glandular epithelium proximally and are entirely glandular distally.

Female: The large ovary extends almost to the tip of the visceral coil and the very thin-walled, narrow upper oviduct opens to the renal oviduct near the base of the bursa copulatrix. No gono-pericardial or reno-gonadial duct were detected in the sections. The renal part of the oviduct is ciliated, very short, and opens to the `common oviduct' at the junction with the short, rather narrow bursal duct.

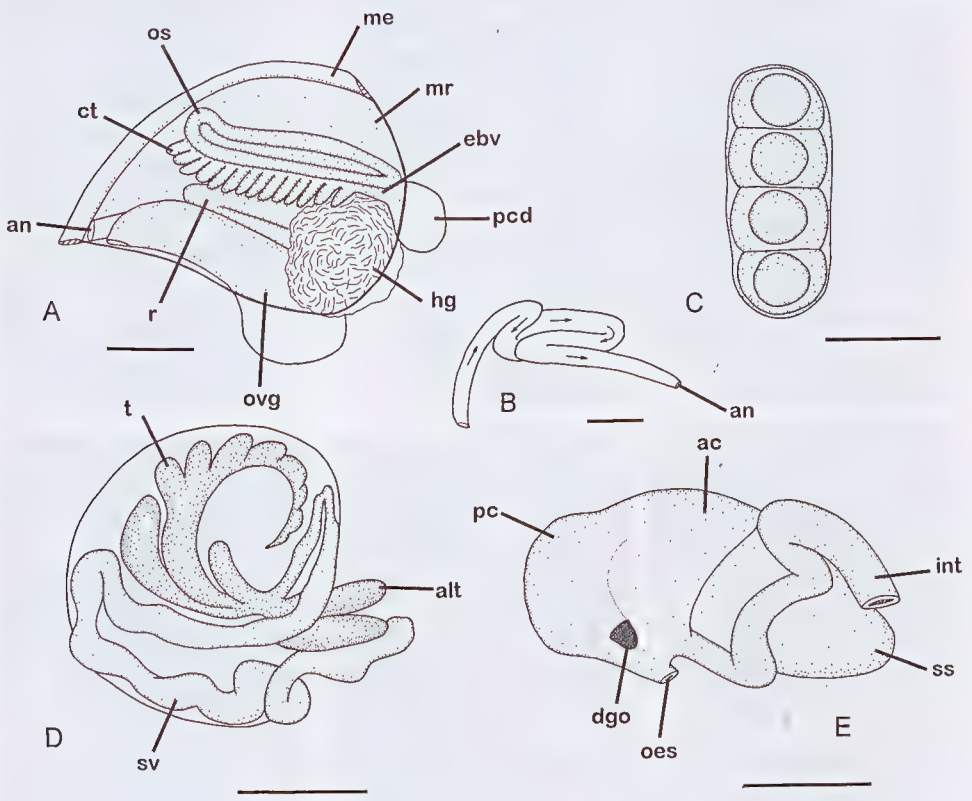

Figure 6.
Anatomy and egg capsules of *C. imitata* n.sp, Mainbar, Port Hacking, NSW. **A** Internal view of roof of mantle (pallial) cavity. **B** Detail of coiling of intestine as seen dorsally. **C** Egg capsules. **D** Testis and seminal vesicle. E Lateral view of stomach. **ac** - anterior chamber of stomach, **alt** - anterior lobe of testis, **an** - anus, **ct** - ctenidium, **dgo** - digestive gland opening, **ebv** - efferent branchial vessel, **hg** - hypobranchial gland, **int** - intestine, **me** - mantle edge, **mr** - mantle roof, **oes** - oesophageal opening to stomach, **os** - osphradium, **ovg** - oviduct gland, **pc** - posterior chamber of stomach, **pcd** - pericardium, **r** - rectum, **ss**- style sac, **sv** - seminal vesicle, **t** - testis. Scales 0.2 mm.

The large, near globular bursa copulatrix (Fig. 7, **br**) lies immediately behind the large oviduct gland (Figs 6A, 7, **ovg**). The bursal walls are lined with short columnar to cuboidal cells and the lumen is packed with sperm. The bursal lumen contains some unorientated sperm but much of the sperm is attached to the epithelium and orientated. It thus appears as though the bursa functions, in part, as a seminal receptacle, as there is no separate seminal receptacle. The large oviduct gland (Fig. 6A, **ovg**, 7) is approximately circular in section in its distal part (Fig. 7A), oval posteriorly (Fig. 7B) and composed of complex, glandular epithelial cells (Ponder, 1988) that are uniform in staining properties (in Cason's trichrome) throughout the gland (there is no separate albumen gland). The oviduct gland lies entirely within the pallial roof and has a thin-walled, ciliated

ventral channel (Fig. 7, **vc**) with a deep ciliated sperm gutter on the left side that continues to the anterior end. The common oviduct opens to this gutter at the posterior end of the oviduct gland, the sperm channel then closing over to form the short, thin-walled bursal duct. The sperm gutter contains sperm and prostatic granules in some specimens suggesting that the penis may deposit sperm anteriorly. Internally the lumen of the gland is a simple slit lined with ciliated epithelium through which the very narrow gland cell ducts pass. The oviduct opening is small and terminal.

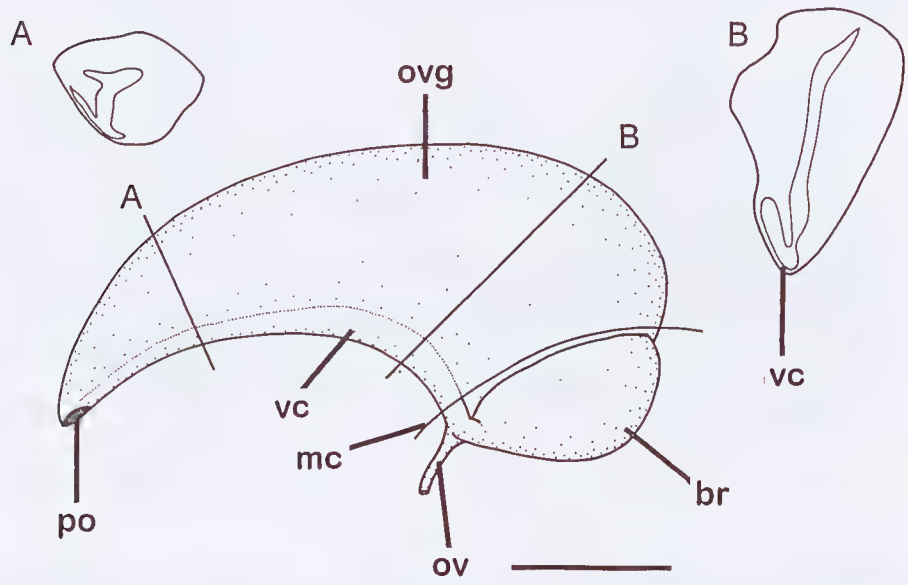

Figure 7.
Female reproductive system of *Calopia imitata* n.sp. viewed from the left side. The lines A and B represent the approximate position of the transverse sections A and B. **br** - bursa copulatrix, **mc** - posterior limit of mantle cavity, **ov** - oviduct, **ovg** - oviduct gland, **po** -pallial opening, **vc** - ventral channel. Scale 0.2 mm.

Nervous system: The large cerebral ganglia situated at the posterior end of the buccal mass are connected by a very short commissure. The cerebro-pleural connectives are even shorter, the pleural ganglia virtually abutting the cerebral ganglia. The supraoesophageal ganglion is small, with a long connective to the right pleural ganglion (about 3-4 times longer than the supraoesophageal ganglion and about twice as long as the right pleural ganglion. The suboesophageal ganglion has a very short connective to the left pleural ganglion (about half the length of the suboesophageal ganglion). The supraoesophageal ganglion is slightly smaller than the suboesophageal ganglion. The short, ovoid pedal ganglia are almost abutting, with a very short connective. None of the ganglia are pigmented.

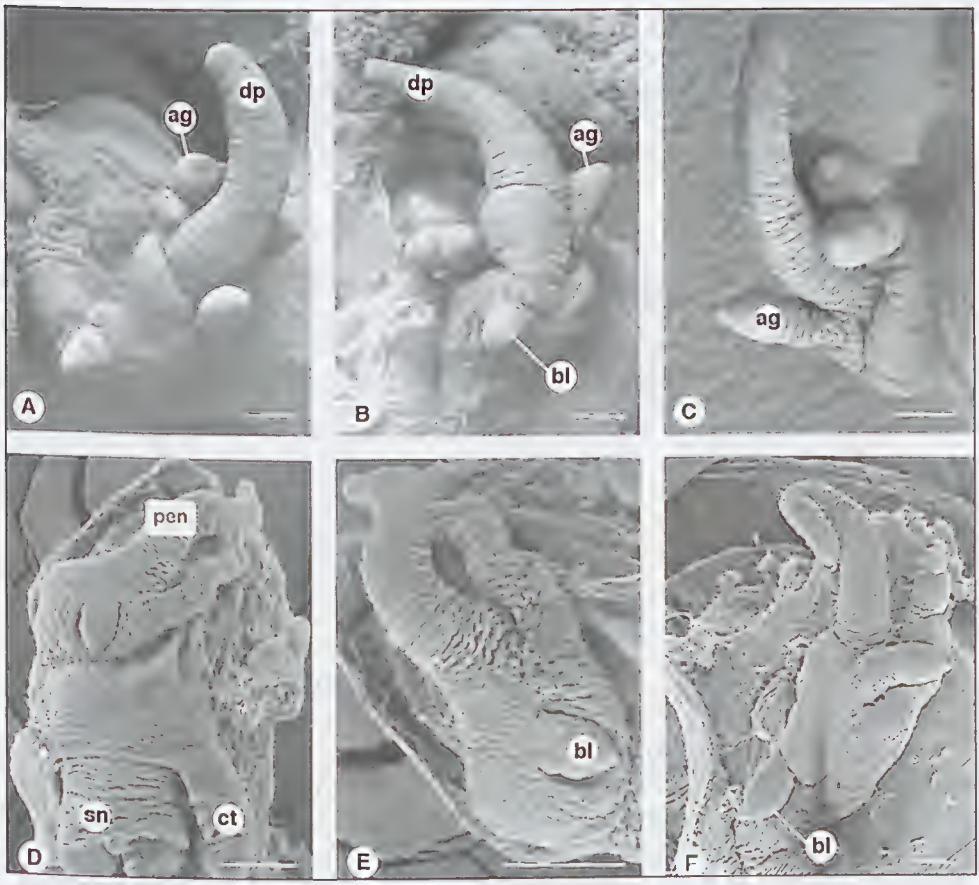

Figure 8.
Head-foot and penes of species of *Calopia*. **A-C** *Calopia imitata* n.sp., Salamander Bay, Port Stephens, NSW, (A) Head and dorsal view of penis, (B) Head, postero-lateral view of penis, (C) Head, anterior view of penis. **D-E** *Calopia minutissima* n.sp. Nightcliff, Darwin, NT, (D) Dorsal view of head-foot and penis, (E) Detail of penis. **F** *Calopia burni* n.sp. Corner Inlet, VIC. Head and anterior to top right of penis. **ag** - apocrine gland, **bl** - basal lobe of penis, **ct** - cephalic tentacle, **dp** - distal portion of penis, **pen** - penis, **sn** - snout. Scale 50 μm.

Reno-pericardial system: As in other rissooideans, the pericardium (Fig. 6A, **pcd**) lies at the posterior end of the pallial cavity, hardly extending into the pallial roof. In fixed material the ventricle is sometimes much smaller than the large, very thin-walled auricle. The renal organ (kidney) is located at the posterior end of the pallial cavity, its anterior wall forming the posterior pallial wall. It is a large, thin-walled sac, its walls mainly lined with a single layer of renal epithelial cells. The renal gland on the outer wall is narrow and simple, running transversely, parallel to the posterior pallial wall. It extends as a white ridge into the kidney lumen, and contains a large afferent renal vessel. The ciliated renal opening lies on the posterior wall of the pallial cavity.

Spawn (Fig. 6C): Specimens collected at Maianbar, Port Hacking, on 24th Nov., 1980 produced several capsules over the next four days which were attached to

the surface of the container. The eggs were laid in rows of capsules, usually 4-7 long (typically four capsules are about 0.43 mm long, five 0.52-0.57 mm), but up to 8. By the first of Dec. shelled veligers were formed in the capsules and were starting to be released (shell diameter 0.14 mm), this continuing for a further 5 days. The capsules are about 0.17 mm in width, the eggs when first laid about 0.09 mm in diameter.

Table 1
Details of eggs and capsules for *Calopia imitata* n.sp., Maianbar, Port Hacking, Nov., 1980.

Number of eggs	Number of capsules laid
3	1
4	9
5	23
6	24
7	21
8	6

Remarks
The new genus is a typical rissooidean, having a taenioglossate radula, a crystalline style, no oesophageal gland and the salivary glands pass over the nerve ring. *Calopia* is a member of the group of taxa having complex histology of the pallial gonoducts and no organic layer on the inside of the shell (the inner `chitinous' layer, Ponder, 1988), including the Vitrinellidae, Assimineidae, Truncatellidae, Hydrobiidae, Bithyniidae, Pomatiopsidae and Falsicingulidae. The absence of a vertical unpigmented ciliated stripe on the right side of the neck and the presence of a horizontal stripe on the left side of the neck are probably synapomorphic for *Calopia*, but no other likely synapomorphies have been identified other than the overall form of the operculum and female reproductive tract. However, *Calopia* differs from members of other rissooidean families in having the following unique combination of characters:- a single metapodial tentacle placed well back on the foot; propodium located behind the dorsal edge of the foot; long compound cilia on the cephalic tentacles; calcareous (?) material in the middle of the otherwise simple operculum that is initially circular; intestine passing around the middle part of the style sac; partial ring of large apocrine glands attached to the middle of the penis; posterior bursa copulatrix; absence of a seminal receptacle; a short, simple renal oviduct; and simple pallial oviduct (not divided into capsule and albumen glands) that lies entirely within the pallial cavity.

The apparently synapomorphic horizontal stripe on the left side of the neck may compensate for the poorly developed gill as it assists in driving water into the pallial cavity, along with the large, strongly ciliated osphradium.

The four species described below are common where they occur and are all very similar. There may be additional taxa represented in the samples of dry

shells in the Australian Museum collections but, given the paucity of useful species-level characters, it will be necessary to carefully examine more living material, and undertake further anatomical study, before the recognition of additional taxa can be justified.

Calopia imitata n.sp.
(Figs 1A-D, 2A,B, 3A, 4, 5A-C, 6, 7, 8A-C, 9, 10A,B, 14)

Derivation: Imitatus, Latin, copy, mimic (refers to the similarity of the shell to other small, conical gastropods).

Type material: Holotype (Fig. 1C) AMS, C 337879. Paratypes AMS, C 316257 (10 dry, many wet); QM (2); NMNHP (2); USNM (2); MONZ (2); LACM (2). Salamander Bay, Port Stephens, NSW, on seagrass in the lower littoral near mouth of small creek. 6 Feb. 1985, W.F.P. & A. Warèn.

Figure 9.
Distribution of *Calopia imitata* n.sp. (♦) and *C. burni* n.sp. (★).

Other material examined (all AMS):

Queensland. Beaches around Mapoon, Gulf of Carpenteria, 11°58'S, 141°53'E, C.Hedley, 23 May 1903, C 328408 (22); Somerset Bay, Cape York Peninsula, 10°44.5'S, 142°35.5'E, W.F.P. & I.Loch, 10 Jul. 1976, C 327335 (2); Alexandra Reef, S of Port Douglas, 16°32'S, 145°31'E, F.H.Plant, 28 Jul. 1973, C 327172 (1); Kurramine Beach, S of Innisfail, 17°47'S, 146°6'E, R.J.Plant, 1972, C 328435 (8); Airlie Beach, near Proserpine, 20°16'S, 148°43'E, F.H.Plant, Aug. 1972, C 327195 (2); Lindeman Is, Whitsunday Passage, 20°27'S, 149°2'E, M.Ward, pre 1935, C 327177 (15); Port Denison, Bowen, 20°4'S, 148°22'E, A.Morton & W.Haswell, pre 1900, C 327150 (1); Bowen, 20°4'S, 148°22'E, J.Laseron, pre 1956, C 327176 (8), pre 1967, C 327189 (4), C 327168 (7); Home Beach, Brampton Is, 20°49'S, 149°17'E, pre 1967, C 327170 (24); Headland between Kings & Queens Beaches, Bowen, 19°59'S, 148°16'E, F.H.Plant, Jun. 1972, C 328400 (7); Edgecumbe Bay, S of Bowen, 20°8'S, 148°23'E, 1959, C 327181 (10); Curtis Is, off Gladstone, 23°38'S, 151°10'E, pre 1958, C 327163 (4), C 327328 (6); Facing Is, Port Curtis, 23°49'S, 151°22'E, J.Laseron, pre 1950, C 327165 (24), pre 1956, C 327448 (4); pre 1967, C 328407 (9);Pialba, Hervey Bay, 25°17'S, 152°50'E, F.H.Plant, Oct. 1972, C 327147 (3); Dundowran Beach, Hervey Bay, 25°18'S, 152°46'E, J.Kerslake, Jul. 1964, C 327190 (1), C 327314 (1), 1959, C 327166 (3), B.Page, C 328260 (13), C 316554 (6); Urangan nr Pialba, 25°18.2'S, 152°54'E, G.A.Clark, 21 Jul. 1987, C 327423 (8); S of Urangan Boat Anchorage, 25°19'S, 152°54'E, I.Loch & B.Duckworth, 24 Oct. 1976, C 327366 (11); Tin Can Bay, NE of Gympie, 25°55'S, 153°1'E, I.Loch & B.Duckworth, 22 Oct. 1976, C 327333 (15), C 327325 (17); Hervey Bay, 25°6'S, 152°49'E, C 316550 (4), J.Laseron, pre 1955, C 327145 (2); S of Urangan Boat Anchorage, Hervey Bay, 25°19'S, 152°54'E, I.Loch & B.Duckworth, 24 Oct. 1976, C 322943 (many); Caloundra beaches, 26°49'S, 153°9'E, J.Kerslake, Aug. 1963, C 327375 (1); NE of Cape Moreton light, 26°54'S, 153°32'E, T.A.Garrard, C 327374 (5); Scarborough, Moreton Bay, 27°12'S, 153°7'E, 1963, C 327360 (3); Moreton Bay, 27°15'S, 153°15'E, J.Laseron, 1955, C 327144 (4), pre 1967, C 327196 (3); Nr Welsby Light, W of Amity Pt, 27°24'S, 153°26'E, CSIRO, 1972, C 327306 (1); Lota, nr Wynnum, Moreton Bay, 27°28'S, 153°11'E, J.Healy, 26 Nov. 1982, C 327326 (many); Manly, Moreton Bay, 27°28'S, 153°11'E, W.F.P., 7 Jan. 1969, C 327359 (many); Dunwich, Stradbroke Is, Moreton Bay, 27°29'S, 153°25'E, W.F.P. & P.H.Colman, 13 Dec. 1969, C 327329 (many); Between Dunwich & Myora, 27°29'S, 153°25'E, W.F.P. & P.H.Colman, 13 Dec. 1969, C 327363 (8); Peel Is, Moreton Bay, 27°30'S, 153°21'E, pre 1950, C 327354 (many), pre 1967, C 327305 (many), pre 1985, C 327356 (many), C 327371 (13); Dunwich, Stradbroke Is, Moreton Bay, 27°30'S, 153°24'E, W.F.P. & P.H.Colman, 11 Dec. 1969, C 327372 (16); Curtis Is, off Gladstone, 23°38'S, 151°10'E, pre 1958, C 328251 (13); Sylvan's Beach, Bellara, Bribie Is, 27°4'S, 153°10'E, G.A.Clark, 20 Jul. 1987, C 167435 (6), 25 Jul. 1987, C 327312 (6), C 327327 (5); Toorbul Point, Ningi, nr Bribie Is., 27°5'S, 153°8'E, G.A.Clark, 25 Jul. 1987, C 167436 (4); Deception Bay, 27°9'S, 153°8'E, pre 1967, C 327331 (10).

New South Wales. Cudgera Creek, Point Hastings, 28°21.6'S, 153°34.3'E, I.Loch & B.Duckworth, 27 Oct. 1976, C 316254 (many); 12km E of Cakora Point, S of Yamba, 29°39.8'S, 153°26.4'E, 22 Feb. 1972, C 316259 (1); Port Stephens, 32°42'S, 152°5'E, 1950, C 316262 (4); Soldiers Point, Port Stephens, 32°42'S, 152°4'E, pre

1967, C 316260 (13), W.F.P. & J.Hall, 24 Oct. 1980, C 316258 (4), 25 Oct. 1980, C 316246 (10); Halifax Bay, Port Stephens, 32°43'S, 152°9.3'E, pre 1959, C 316274 (2); Nelson Bay, Port Stephens, 32°43.3'S, 152°8.7'E, W.F.P., 27 Jan. 1971, C 328434 (6); Salamander Bay, Port Stephens, 32°43.14'S, 152°5.43'E, W.F.P. & J.Hall, 26 Oct. 1980, C 316253 (many); Patonga, Broken Bay, 33°33'S, 151°16'E, circa 1950, C 316267 (2); Off Patonga Beach, Broken Bay, 33°33.6'S, 151°16.8'E, C.Laseron, pre 1959, C 316263 (11); Pittwater, Broken Bay, Sydney, 33°37'S, 151°18'E, circa 1950, C 316266 (many), C 316261 (13); Careel Bay, Pittwater, Sydney, 33°37.3'S, 151°19.5'E, P.A.Hutchings, 6 Sep. 1973, C 316264 (4), C 316251 (11), W.F.P., Jul. 1997, C 328401 (many); Salt Pan Cove, Newport, Pittwater, 33°39'S, 151°18.3'E, W.F.P., 28 Dec. 1974, C 328433 (3); Bayview, Pittwater, 33°39.6'S, 151°17.7'E, circa 1955, C 316265 (3); Bobbin Head Bay, Hawkesbury River, 33°39.6'S, 151°9.5'E, J.Voorwinde, circa 1955, C 316270 (9); Narrabeen Lagoon, Sydney, 33°42.6'S, 151°16.7'E, J.Kerslake, Jun. 1971, C 316268 (1); North Harbour, Sydney, 33°48'S, 151°16.3'E, W.F.P. & J.Hall, 20 Apr. 1982, C 316271 (many); The Spit, Middle Harbour, 33°48.3'S, 151°14.4'E, circa 1955, C 316272 (7); Quarantine Bay, North Head, Sydney, 33°49'S, 151°17'E, 1950, C 316505 (2); North Head, Sydney Harbour, 33°49'S, 151°17'E, W.F.P. & J.Voorwinde, 9 Mar. 1969, C 316508 (2); Middle Harbour, Sydney, 33°49'S, 151°15'E, C.Hedley, Starkey & H.L.Kesteven, pre 1911, C 32469 (1); Sydney Harbour, 33°51'S, 151°14'E, pre 1903, C 11013 (9); Off Morts Dock, Balmain, 33°51.4'S, 151°11'E, D.F.McMichael & J.C.Yaldwyn, 22 Oct. 1963, C 316269 (many); Cooks River, 33°55.5'S, 151°8.5'E, circa 1900, C 316510 (13); Botany Bay, Sydney, 33°59'S, 151°12'E, J.Voorwinde, 1955, C 316509 (3); Dolls Point, Georges River, 34°0'S, 151°9'E, pre 1950, C 328438 (3); Ocean Beach, Kurnell, 34°0.58'S, 151°12.38'E, 1950, C 316275 (2); Kurnell, Botany Bay, 34°0.58'S, 151°12.38'E, W.F.P., 21 Apr. 1979, C 316507 (many); Silver Beach, Kurnell, 34°0.63'S, 151°12.21'E, 1979, C 316256 (many); Towra Point, Botany Bay, 34°2'S, 151°9'E, L.Sekuljica, 16 Sep. 1997, C 336333 (2); Cronulla, Sydney, 34°3'S, 151°10'E, pre 1967, C 316276 (many); Gunnamatta Bay, Port Hacking, 34°3.95'S, 151°8.55'E, pre 1967, C 316277 (11); South West Arm, Port Hacking, 34°4.4'S, 151°6.3'E, W.F.P., 9 Aug. 1975, C 316504 (1); Ship Rock, Port Hacking, 34°4.42'S, 151°7.6'E, W.F.P. & S. Rainer, 9 Oct. 1975, C 316506 (1); Gogerleys Point, Port Hacking, 34°4.5'S, 151°6.3'E, W.F.P., 7 Oct. 1990, C 328437 (10); Port Hacking, Sydney, 34°4.8'S, 151°7.47'E, W.F.P. & A.Warèn, 21 Dec. 1984, C 316552 (8), C 316553 (2); Fishermans Bay, Port Hacking, 34°4.8'S, 151°7.47'E, W.F.P., 17 Sep. 1978, C 316244 (many); Outer Cabbage Tree Basin, Port Hacking, 34°4.82'S, 151°7.85'E, W.F.P. & A.Warèn, 21 Dec. 1984, C 316511 (5); Simpsons Bay, Port Hacking, 34°5'S, 151°8'E, W.F.P., 10 Aug. 1975, C 316503 (1); C 316247 (6) & 17 Sep. 1978, C 316502 (11); Maianbar, Port Hacking, 34°5'S, 151°7.8'E, W.F.P. & J.Hall, 24 Nov. 1980, C 316252 (1), W.F.P. & A.C.Miller, 4 Sep. 1990, C 316250 (11), W.F.P. & I.Loch, 16 Apr. 1980, C 316248 (18), W.F.P. & J.Hall, 24 Nov. 1980, C 316255 (many); The Basin, Simpsons Bay, 34°5'S, 151°8'E, W.F.P., 10 Aug. 1975, C 316245 (3); Simpsons Bay, Port Hacking, 34°4.72'S, 151°8.32'E, W.F.P. & B.S.Morton, 22 Sep. 1972, C 316249 (many); Batemans Bay, 35°43'S, 150°12'E, circa 1950, C 316273 (4); Merimbula Lake, Merimbula, 36°53.7'S, 149°55'E, W.F.P. & G.A.Clark, 28 Nov. 1989, C 328436 (1); Pambula Lake, 36°58.4'S, 149°53.35'E, J.H.Day & party, 4 Oct. 1975, C 329675 (2).

Table 2
Shell dimensions of *Calopia imitata* n.sp.

	SL	SW	AL	AW	WH
Holotype	2.13	1.44	0.35	0.76	5.10
Figured paratype	1.63	1.27	0.75	0.63	4.75
Figured specimens					
C 316251, Pittwater, Qld	1.95	1.57	0.99	0.81	4.50
C 322943, Hervey Bay, Qld	1.32	1.13	0.68	0.53	3.75
C 328408, Mapoon, Qld	1.40	1.09	0.65	0.47	4.50
Paratypes AMS, C 316257 (n=20)					
Min	1.51	1.16	0.66	0.60	4.25
Max	2.23	1.47	0.84	0.79	4.75
Mean	1.822	1.305	0.758	0.681	4.548
SD	0.157	0.081	0.051	0.051	0.160
Hervey Bay, Qld. AMS, C 322943 (n=8)					
Min	1.26	1.06	0.64	0.54	3.10
Max	1.86	1.29	0.82	0.66	4.60
Mean	1.495	1.141	0.705	0.590	4.194
SD	0.180	0.081	0.061	0.044	0.464
Mapoon, Qld. AMS, C 328408 (n=4)					
Min	0.92	0.82	0.52	0.46	3.40
Max	1.20	0.97	0.66	0.54	4.20
Mean	1.095	0.897	0.597	0.500	3.800
SD	0.126	0.063	0.064	0.041	0.365
Bowen, Qld. AMS, C 339278 (n=2)					
Min	1.29	1.08	0.60	0.52	3.75
Max	1.50	1.17	0.78	0.67	4.25
Mean	1.395	1.125	0.690	0.595	4.000
SD	0.148	0.064	0.127	0.106	0.354

Diagnosis: Shell large for genus, up to about 2.2 mm in length (usually slightly less than 2mm), conical, with very narrowly open umbilicus or umbilical slit. Penis with 5-8 apocrine glands and glandular lobe on base.

Description:
Shell (Fig. 1 A-D): Small (up to 2.23 mm in length), conical, smooth, of up to 4.75 weakly convex whorls. Aperture partially separated from body whorl, sub-pyriform, angled posteriorly, rounded anteriorly. Base with narrow umbilicus, or umbilicus closed and represented by slit (also in subadults), width about 5-10% of maximum shell width, not distinctly set off from base, at best bordered by weak subangulation, sculptured with rather indistinct axial rugae within. Base sculptured with few (2-5) low spiral ridges on lower half. Peristome thin, simple. Periostracum thin, transparent, shell white.

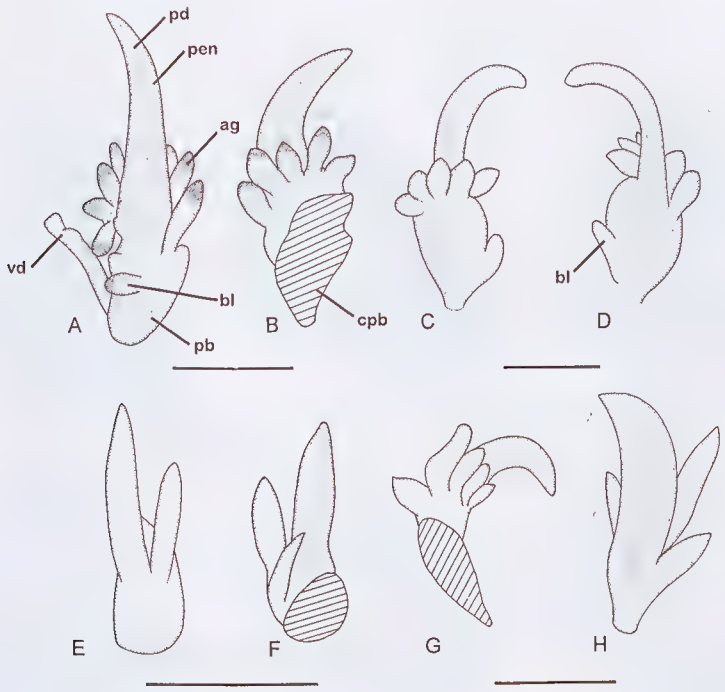

Figure 10.
Penes of *Calopia* species. **A-B** *Calopia imitata* n.sp. Maianbar, Port Hacking, NSW. **C-D** *Calopia burni* n.sp. Port Welshpool, Corner Inlet, VIC. **E-F** *Calopia minutissima* n.sp. Nightcliff, Darwin, NT. **G-H** *Calopia laseroni* n.nam. Mission Bay, near Broome, WA. **ag** - apocrine gland, **bl** - basal lobe of penis, **cpb** - cut base of penis, **pb** - base of penis, **pen** - distal part of penis, **pd** - penial duct, **vd** - vas deferens. Scales 0.2 mm.

Operculum (Fig. 2A,B): Oval, as for genus.

Head-foot (4, 5A-C): Snout irregularly pigmented with dark grey patches laterally, otherwise whitish (due to rather dense cream pigment spots); distal end weakly bilobed, transparent. Length of cephalic tentacles equal to approximately half the width of last whorl of shell; transparent with numerous cream spots and black band (up to about quarter of tentacle length in width, but usually narrower) at about distal third, proximal end dark grey to black laterally, lacking cream pigment spots; unpigmented immediately around eye; distal end expanded, with long `setae' (compound cilia) (Fig. 4 A-D, H, **cc**). Ventrally cephalic tentacles unpigmented, with dorsal white pigment showing through otherwise transparent tentacle. Ciliation patterns of tentacles and snout described above. Head with dense cream pigment spots dorsally, lacking distinct `eyebrow'; right side of neck uniformly dark grey-brown above junction with foot, left side with unpigmented, crescent-shaped ciliated horizontal stripe. Foot translucent white, with four pigmented areas laterally - one bordering edge of propodium, another just behind anterior patch on each side of foot, third area just behind this patch and largely anterior to opercular lobe, and fourth

(sometimes absent) largely behind opercular lobe. Posterior part of foot tapering, end variable, from slightly indented, rounded to narrowly rounded. Metapodial tentacle raised at about 45°. Mantle edge especially strongly ciliated in darkly pigmented posterior corner. Animal visible through shell; mantle cavity roof variably mottled dark grey to dark reddish-brown and cream to pale yellow, visceral coil with mainly dark reddish-brown and black pigment, with yellow, mainly vertical, streaks.

Radula (Fig. 3A): As for genus. Central 2(-3)+1+2(-3), median cusp parallel-sided with blunt, denticulate end; lateral 2-3+1+4-6, primary cusp blunt with rounded end; inner marginal teeth with 14-19 cusps, outer marginal teeth with many small cusps (number undetermined).

Penis (8A-C, 10A,B): Transparent, with 5-8 apocrine glands beneath central portion; short glandular lobe at base. Basal portion (quarter to third of penis length) markedly broader than long slender, tapering distal part.

Distribution (Fig. 9): East coast of Australia and (tentatively) the western side of Cape York.

Remarks: Surprisingly, this common taxon does not appear to have been previously named, possibly because the shell is readily confused with other small, white conical taxa. There is considerable variation in shell size and shape in this species in many populations and especially in those from tropical coastal Queensland. An example of an elongate form resembling (and tentatively identified as) *C. imitata* from Mapoon, Gulf of Carpentaria is figured for comparison (Fig. 11I). Some samples from eastern Queensland, for example one from Hervey Bay, have shell forms that range continuously from typical *C. imitata* to shells resembling the species named *C. laseroni* n.nam. below. While a number of intergrading morphs can be recognised in this population (AMS, C 322943) the smaller *C. laseroni*-like morph cannot be separated with confidence from a large broad, distinctly umbilicate morph (Fig. 1D) which is very similar to some broad specimens of *C. imitata* from NSW. Another morph is small and more narrowly conical. Unfortunately I have not been able to examine living material to determine whether this variation represents two or more sympatric species or simply variability within a single taxon.

Calopia burni n.sp.
(Figs 1E,F, 3F, 8F, 9, 10C,D, 12A,C, 14)

Cyclostrema contabulata var.; Pritchard and Gatliff, 1902: 100 (*non* Tate, 1899).

Derivation: Named for Mr Robert (Bob) Burn, Geelong, Victoria as a small recognition of his considerable contributions to malacology.

Type material: Holotype (Fig. 1F) AMS, C 337883. Paratypes AMS, C 327378 (12 dry, many wet); MV (4). Jetty at Stony Point, Western Port, Victoria; on *Zostera* at low tide on sand/mud flat in shallow pool. 28 Feb. 1977. W.F. Ponder.

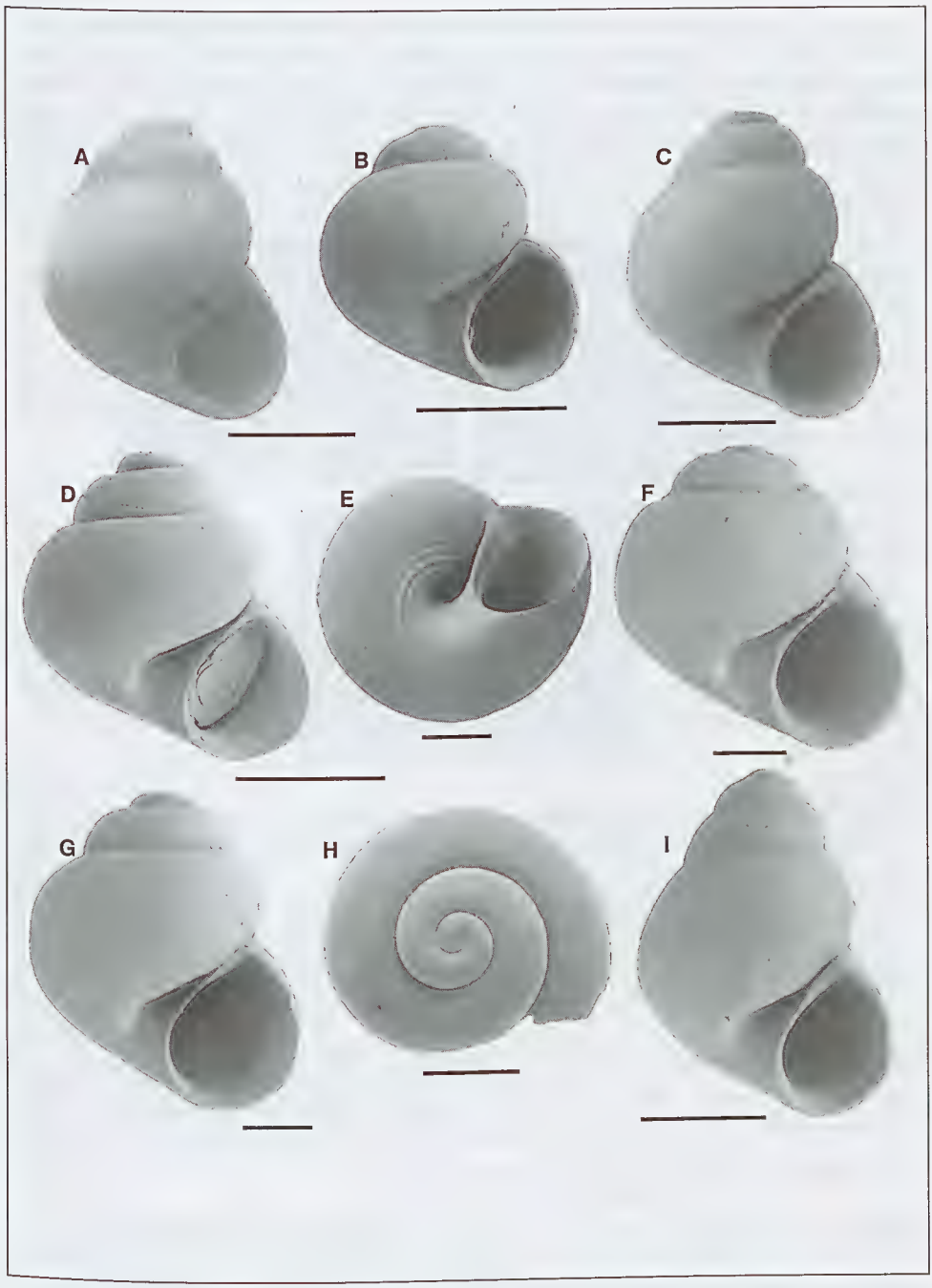

Figure 11.
Shells of *Calopia* species. **A-C, E** *Calopia laseroni* n.nam. (A) Lectotype, Darwin, NT (C 337930), (B) Mission Bay, near Broome, NWA, WA (C 337887), (C) Facing Is., Port Curtis, QLD (C 322945), (E) N. side, East Pt, Darwin, NT (C 327295). **D, F-H** *Calopia minutissima* n.sp. (D) Holotype, Nightcliff, Darwin, NT (C 337878), (F) Somerset Bay, Cape York Peninsula, QLD (C 328405), (G) Facing Is, Port Curtis, QLD (C 328406), (H) Dorsal view, paratype, Nightcliff, Darwin, NT (C 330800). **I** *Calopia* cf. *imitata*. Beaches around Mapoon, Gulf of Carpentaria, NT (C 328408). Scales A-D, I 500 μm, E-H 200 μm.

Other material examined (AMS, unless otherwise indicated): Victoria. Western Port, 38°26'S, 145°13'E, C.J.Gabriel, (as *C. contabulata*), C 337806 (8); Cannons Ck, Port Phillip Bay, 38°13'S, 145°19'E, C 327379 (6); Warneet, Western Port 38°14'S, 145°19'E, W.F.P. & B.J.Smith, 15 Feb. 1969, C 327419 (2); N of Churchill Is & Newshaven, Western Port, 38°27.15'S, 145°20.9'E, W.F.P., 28 Feb. 1977, C 327420 (3); Shoreham, Western Port, 38°27.5'S, 145°3'E, pre 1975, SAM TD60 (7); Western Port Bay, 38°22'S, 145°32'E, G.Dare, C 327377 (4); Northern shore of Corner Inlet, 38°42'S, 146°27'E, W.F.P. & G.A.Clark, 10 Feb. 1987, C 327421 (15); Sandy Pt, Foreshore Reserve, 38°50.6'S, 146°8.67'E, J.H.Waterhouse & G.A.Clark, 9 Dec. 1988, C 328225 (17).

Diagnosis: Shell large for genus (up to 1.67 mm in length), ovate, with prominent open umbilicus. Penis with 4-5 apocrine glands and small glandular lobe on base.

Description:
Shell (Figs 1E, F, 12A,C): Small (up to 1.67 mm in length), ovate, smooth, of up to 4.25 weakly convex whorls. Aperture largely separated from body whorl, sub-pyriform, angled posteriorly, rounded anteriorly. Base with moderately wide, open umbilicus, about 15% of maximum diameter of shell (much narrower in juveniles); umbilicus not distinctly bordered and with weak axial growth lines internally. Base sculptured with 3-7 distinct, narrow spiral ridges on lower half. Peristome thin, simple. Periostracum thin, transparent, shell white.

Table 3
Shell dimensions of *Calopia burni* n.sp.

	SL	SW	AL	AW	WH
Holotype C 337883	1.62	1.38	0.77	0.67	4.30
Paratypes C 327378 (n=20)					
Min	1.34	1.16	0.66	0.58	3.60
Max	1.67	1.42	0.84	0.72	4.25
Mean	1.498	1.277	0.748	0.643	4.017
SD	0.106	0.070	0.046	0.041	0.179

Operculum (Fig. 2A,B): Oval, as for genus.

Head-foot: Living animal similar to that of *C. imitata*, but details not recorded.

Radula (Fig. 3F): Very similar to that of *C. imitata*. Central 2-3+1+2-3, median cusp parallel-sided with blunt, denticulate end; laterals 2-3+4-5, primary cusp tapering with blunt end; inner marginal teeth with 12(?)-18 cusps; outer marginal teeth with ca. 11 cusps.

Penis (Fig. 8F, 10C,D): Similar to that of *C. imitata*, with 4-5 apocrine glands and small basal lobe.

Distribution (Fig. 9): Embayments on mid Victorian coast.

Remarks: The shell of this species is about the same size as *C. imitata* but is more ovate and adults have a wider umbilicus. The two species are geographically separated as there appears to be a gap in eastern-most Victoria where *Calopia* does not occur, despite the presence of considerable suitable habitat in the vicinity of Lakes Entrance and Malacoota.

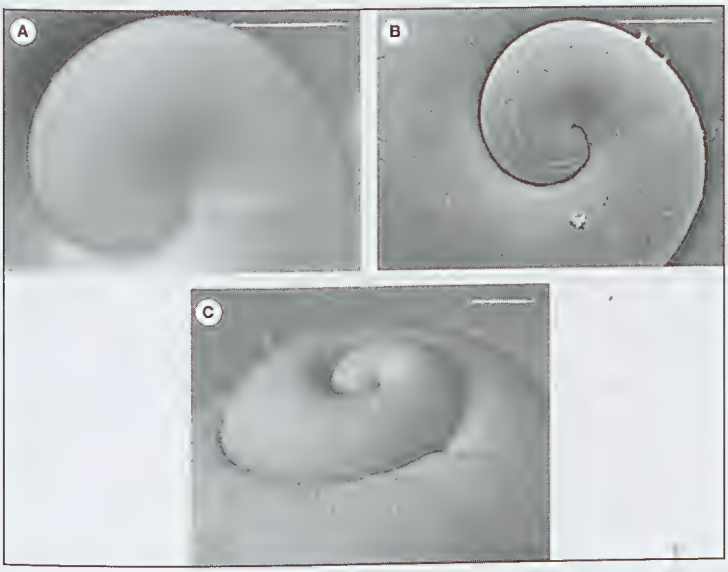

Figure 12.
Protoconchs of *Calopia* species. **A,C** *Calopia burni* n.sp.. Jetty at Stony Pt., Westernport, VIC (C 327378). **B** *Calopia minutissima*. Nightcliff, Darwin, NT (C 330800). Scale 50 μm.

Calopia laseroni new name
(Figs 2C, 3B, 10G,H, 11A-C,E, 13, 14)

Lucidestea perforata Laseron, 1956:449, fig. 170, not *Rissoa perforata* Thiele, 1925, a species of *Lucidestea*.
Type material: Darwin. Lectotype (here chosen) (Fig. 11A) (AMS, C 337930) and 3 paralectotypes [AMS, C 102481, C 109005 (one badly corroded specimen possibly *C. minutissima*)]. One additional paralectotype is *C. minutissima* (C 328221).

Other material examined (all AMS):
Western Australia. Mission Bay, near Broome, 14°7'S, 126°42'E C 337887 (9); Broome, 17°58'S, 122°14'E, B.Duckworth, 23 Jun. 1980 C 327424 (17); Port Hedland, 20°18'S, 118°35'E, M.Seymour, pre 1950, C 327428 (4); Six Mile Creek, Port Hedland, 20°50'S, 120°36'E, M.Seymour, Oct. 1974, C 327429 (15); Beagle Is, Mary Ann Group, Onslow, 21°12'S, 115°38'E, F.H.Plant, Sep. 1970, C 327425 (many); Exmouth Gulf, SE of Exmouth, 22°24'S, 114°8'E, W.F.P., 20 Jan. 1972, C 327427 (7); Freycinet Reach, Shark Bay, 26°3'S, 113°26'E, B.R.Wilson & G.W.Kendrick, 4 Mar. 1964, C 328397 (8).

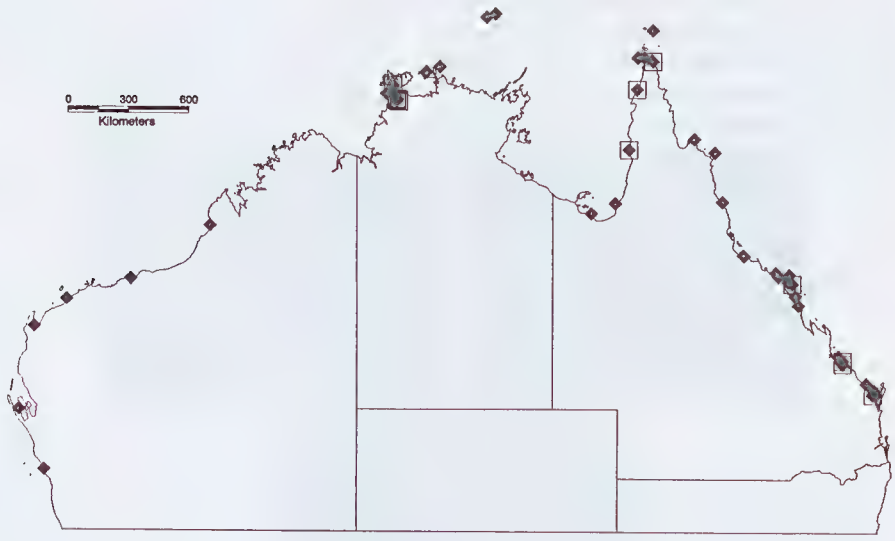

Figure 13.
Distribution of *Calopia laseroni* n.nam. (♦) and *C. minutissima* n.sp. (□)

Northern Territory. 2km off Point Charles, Darwin, 12°10′S, 130°22′E, M.Ward, 14 Jul 1938, C 327293 (2); Buchanan Is, S side of Melville Is, 11°49′S, 130°39′E, N.Kamper, 2 Dec. 1938, C 328231,(many), C 327125 (1), C 327449 (many); Off Emery Point, Darwin, 12°27′S, 130°49′E, P.H.Colman, 25 Oct. 1969, C 327296 (18); Fannie Bay, Darwin, 12°26′S, 130°49′E, W.F.P., 14 Jul. 1988, C 330801 (5); East Point, Darwin, 12°25′S, 130°49′E, W.F.P., 14 Jun. 1976, C 327277 (1), B.W.Jenkins, 29 Jun. 1983, C 327278 (3), C 327295 (5); Nightcliff, Darwin, 12°23′S, 130°50′E, W.F.P., 15 Jul. 1988, C 328264 (6), C 330799 (8), C 330803 (25), C 328439 (1), C 330797 (5); Ludmilla Creek, East Point, Darwin, 12°25′S, 130°50′E, W.F.P., 14 Jun. 1976, C 327280 (2); Darwin, 12°28′S, 130°50′E, J.Laseron, circa 1940, C 327288 (1), C 102481 (1), C 109005 (3); Port Darwin, 12°28′S, 130°50′E, J.Laseron, circa 1940, C 327300 (1), C 328404 (6); Caiman Ck, Berkeley Bay, 11°13′S, 132°11′E, W.F.P. & G.Beckensale, 2 Jun. 1976, C 327441 (1), C 327303 (many); Oxley Is, 11°0′S, 132°49′E, J.K.Lowry, 21 Oct. 1982, C 327279 (16); 365km N of Milingimbi Is, Arnhem Land, 8°48′S, 134°58′E, P.H.Colman, 18 Oct. 1969, C 327290 (2); Arnhem Land, 8°39′S, 135°21′E, 15 Oct. 1969, C 327302 (4).
Queensland. Off Albert River mouth, Gulf of Carpenteria, 17°24′S, 139°47′E, D.F.McMichael & J.C.Yaldwyn, 7 Dec. 1963, C 327159 (1); 6 miles W of Van Diemans Inlet, Gulf of Carpentaria, 16°58′S, 140°53′E, C.Hedley, 5 Jun. 1903, C 15360 (1); ca. 2 miles off Horsey R. mouth, Gulf of Carpentaria, 14°35′S, 141°30′E, C.Hedley, 3 Jun. 1903, C 328254 (6), C 327447 (2); Beaches around Mapoon, Gulf

of Carpenteria, 11°58'S, 141°53'E, C.Hedley, 23 May 1903, C 322947 (many); Gannet Passage, Torres Strait, 10°35'S, 141°55'E, 9 Sep. 1874, C 327155 (1), C 327431 (1); Gannet Passage, NNE of Booby Is, 10°36'S, 141°55'E, 9 Sep. 1874, C 327194 (4), C 327437 (4); Muddy Bay, Thursday Is, Torres Strait, 10°35'S, 142°13'E B.Goldman, 6 Mar. 1972, C 327153 (1); Albany Passage, Cape York, 10°43'S, 142°34'E, M.Ward, Sep. 1928, C 327433 (5); Somerset Bay, Cape York Peninsula, 10°44.5'S, 142°35.5'E, W.F.P. & I.Loch, 10 Jul. 1976, C 327151 (3), C 322944 (6); S side of Fly Point, Somerset, Cape York Peninsula, 10°45'S, 142°36'E, W.F.P. & I.Loch, 11 Jul. 1976, C 328248 (1); Saibai Village, Saibai Is, Torres Strait, 9°22'S, 142°36'E, W.F.P. & I.Loch, 7 Jul. 1976, C 327161 (1); South Is, Lizard Is, GBR, 14°42'S, 145°27'E, W.F.P., 16 Jan. 1980, C 327179 (1); Pipon Is, 14°7'S, 144°31'E, J.Brazier, 11 Jun. 1875, C 327175 (1); Cairns Harbour, 16°53'S, 145°48'E, pre 1967, C 327191 (1); Cape Pallarenda Beach, Townsville, 19°12'S, 146°46'E, F.H.Plant, Aug. 1972, C 327435 (7); Rowes Bay, Townsville, 19°14'S, 146°48'E, I.Loch, 31 May 1977, C 327123 (1); Headland between Kings & Queens Beach, Bowen, 19°59'S 148°16'E, F.H.Plant, Jun. 1972, C 322946 (many); Lindeman Is, Whitsunday Passage, 20°27'S, 149°2'E, M.Ward, pre 1935, C 327149 (1); Paradise Bay, Long Is., 20°23'S, 148°51'E, J.Hewitt, Dec. 1969, WAM 749-85(1); Hayman Is, Whitsunday Ids, 20°3.6'S, 148°53.5'E, C 327124 (1); Bowen, 20°4'S, 148°22'E, J.Laseron, pre 1956, C 328233 (9), C 327443 (16), pre 1967, C 327198 (1), C 328229 (3); Edgecumbe Bay, S of Bowen, 20°8'S, 148°23'E, 1959, C 327444 (4), C 327434 (10); Shoal Point, Mackay, 21°0'S, 149°10'E, F.H.Plant, Jun. 1972, C 327439 (4), C 327188 (7), C 327154 (14), 29 Jun. 1973, C 327148 (2); Sarina Beach, S of Mackay, 21°24'S, 149°19'E, B.Page, pre 1950, C 328432 (2); Curtis Is, off Gladstone, 23°38'S, 151°10'E, pre 1958, C 327438 (1); Facing Is, Port Curtis, 23°49'S, 151°22'E, J.Laseron, pre 1950, C 328234 (36), C 327446 (3), pre 1967, C 322945 (many); Barney Point, Port Curtis, 23°50'S, 151°16'E, Dr. H.L.Kesteven, circa 1917, C 327440 (1); Tannum Sands, Port Curtis, 23°57'S, 151°22'E, B.Page, 1969, C 328252 (6); Bargara, nr Bundaberg, 24°49'S, 152°28'E, L.Harford, May 1948, C 327450 (1); Gattakers Bay, Hervey Bay, 25°16'S, 152°48'E, N. & V.Gomersall, Jun. 1963, C 327158 (2); Pialba, Hervey Bay, 25°17'S, 152°50'E, F.H.Plant, Oct. 1972, C 327162 (2), C 328228 (19); Urangan nr Pialba, 25°18.2'S, 152°54'E, G.A.Clark, 21 Jul. 1987, C 328240 (1); Dundowran Beach, Hervey Bay, 25°18'S, 152°46'E, B.Page, C 328261 (many); Hervey Bay, 25°6'S, 152°49'E, C 316551 (10), J.Laseron, pre 1955, C 327436 (2), C 327146 (3).

Diagnosis: Shell medium-sized for genus, up to about 1.33 mm in length (usually slightly less than 1.2 mm), broadly ovate, with wide, open umbilicus. Penis with 5 apocrine glands and no glandular lobe on base.

Description:

Shell (Fig. 11A-C, E): Small (up to 1.33 mm in length), broadly ovate, smooth, of up to 4.5 (usually less than 4) weakly convex whorls. Aperture largely separated from body whorl, sub-pyriform, angled posteriorly, rounded anteriorly. Base with wide, open umbilicus, about 15% of maximum diameter of shell; sculptured with a few distinct spiral grooves on lower half. Peristome thin, simple. Periostracum thin, transparent, shell white.

Table 4
Shell dimensions of *Calopia laseroni* n.nam.

	SL	SW	AL	AW	WH
Lectotype	1.21	1.00	0.54	0.48	4.25
Paralectotypes					
C 109005	1.10	1.03	0.55	0.47	4.00
	1.01	0.95	0.54	0.47	4.20*
C 102481	1.59	1.27	0.71	0.58	4.75**
C 328221	1.04	0.93	.	.	3.75***
Figured specimens					
Mission Bay, Broome, WA, C 337887	0.97	0.90	0.52	0.45	3.80
East Point, Darwin, NT, C 327295	0.86	0.87	0.47	0.41	3.70
Facing Is., Port Curtis, Qld, C 322945	0.92	0.84	0.47	0.40	3.40
Topotypes					
Port Darwin, NT. AMS, C 328404 (ex Laseron) (n=4)					
Min	1.01	0.93	0.52	0.44	3.80
Max	1.23	1.02	0.57	0.50	4.25
Mean	1.095	0.975	0.545	0.465	4.012
SD	0.096	0.037	0.021	0.026	0.246
Misson Bay, Broome, WA. AMS, C 327424 (n=6)					
Min	0.91	0.86	0.49	0.43	3.25
Max	1.12	0.97	0.53	0.50	3.50
Mean	0.988	0.915	0.518	0.463	3.417
SD	0.075	0.041	0.016	0.027	0.129
East Point, Darwin, NT. AMS, C 327295, C 327277 (n=8)					
Min	0.86	0.82	0.45	0.40	2.80
Max	1.08	1.02	0.58	0.54	3.75
Mean	0.970	0.925	0.513	0.459	3.394
SD	0.089	0.082	0.052	0.047	0.308
Mapoon, Qld. AMS, C 322947 (n=5)					
Min	1.03	0.91	0.54	0.44	3.65
Max	1.33	1.07	0.60	0.50	4.50
Mean	1.174	0.972	0.564	0.462	4.120
SD	0.115	0.067	0.023	0.024	0.375
Facing Island, Port Curtis, Qld. AMS, C 322945 (n=9)					
Min	0.84	0.77	0.44	0.38	3.25
Max	0.99	0.90	0.52	0.44	3.75
Mean	0.930	0.834	0.478	0.410	3.583
SD	0.041	0.035	0.025	0.018	0.171
Bowen, Qld. AMS, C 322946 (n=8)					
Min	1.06	0.91	0.49	0.41	3.75
Max	1.20	0.98	0.57	0.47	4.20
Mean	1.130	0.947	0.541	0.444	4.025
SD	0.047	0.024	0.025	0.021	0.169

	SL	SW	AL	AW	WH
Hervey Bay, Qld. AMS, C 322943 (n=2)					
Min	1.10	0.85	0.57	0.47	3.80
Max	1.22	0.95	0.61	0.50	4.00
Mean	1.160	0.900	0.590	0.485	3.900
SD	0.085	0.071	0.028	0.021	0.141
Cape York, Qld. AMS, C 322944	1.04	0.95	0.50	0.42	4.00

* (badly affected by 'bynes'disease - possibly *C. minutissima* n.sp.)
** (this specimen is much larger than any other seen - although it appears to be a geronic (possibly due to parasitism) specimen of *C. laseroni*. Treated as unknown in Fig. 14).
***(a large, slightly damaged specimen of *C. minutissima*).

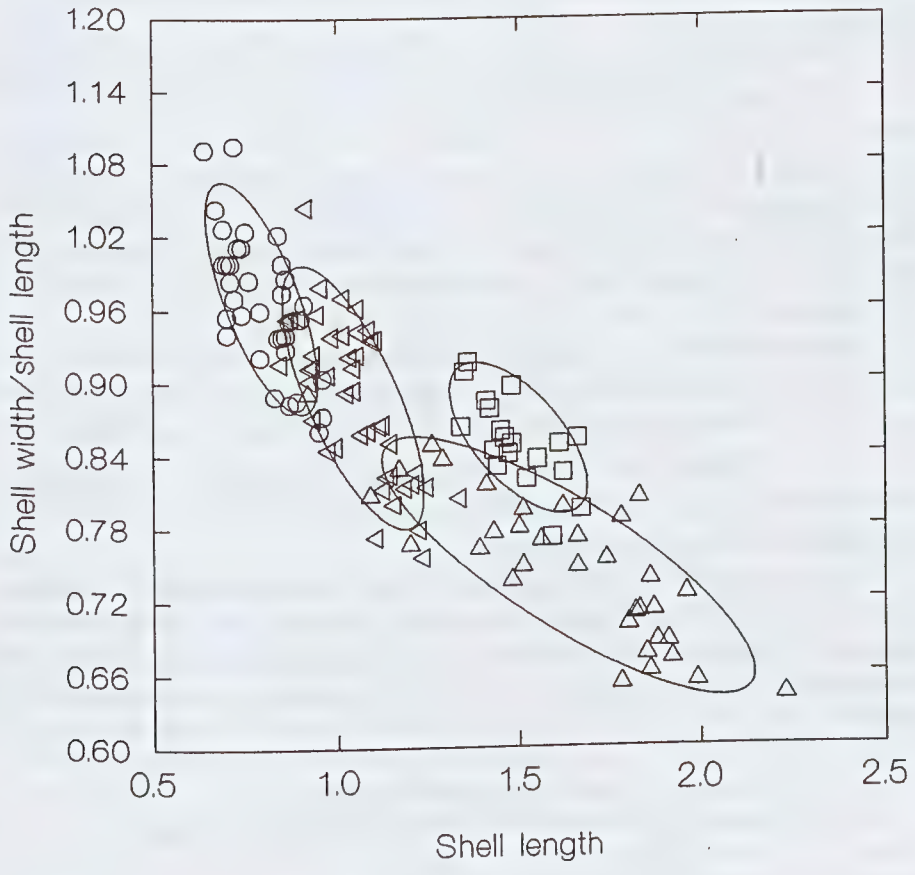

Figure 14.
Plot of shell length against shell width/shell length with 75% bivariate ellipsoids shown for each species. *C. imitata* (△), *C. burni* (□), *C. laseroni* (◁), *C. minutissima* (○).

Operculum (Fig. 2F): As for genus.

Radula (Fig. 3B): As for genus. Central 2+1+2, median cusp pointed; lateral 2+1+3-4, primary cusp tapering, rather blunt; inner marginal teeth with 10-12 cusps, outer marginal teeth with minute cusps (number undetermined).

Penis (Fig. 10G,H): With terminal section parallel-sided for most of length, tapering terminally; with straight central penial duct. Five apocrine glands situated at middle part of penis on lower surface (when at rest), two and part of a third visible from above. No basal lobe present and base not markedly wider than terminal part.

Distribution (Fig. 13): Northern half of Australia.

Remarks: Most of the specimens from Darwin are empty shells, and there was inadequate material to investigate the animal. However a sample that was very similar (in shell characters) to the types was available for dissection from Mission Bay, near Broome, NWA. A specimen from this latter lot (Fig. 11B) is illustrated for comparison with the lectotype (Fig. 11A), as well as specimens from East Point, Darwin (Fig. 11E) and Queensland (Fig. 11C). The penis (two specimens examined from near Broome) are similar to the two species described above in that there are five apocrine glands, the largest markedly larger in one specimen, but only about a third of the penial length compared with about half in the other specimen. The penis of *C. laseroni* differs from *C. imitata* and *C. burni* in that the base is more slender and apparently lacks a basal glandular lobe. Three of the apocrine glands are visible dorsally in the retracted penis and all five from below.

Some specimens from tropical Queensland are similar in shell characters to this species but inadequate preserved material is available to determine whether or not the penial characters are similar. As noted above, some shells from Queensland are difficult to determine if they are this species or small, inflated individuals of *C. imatata*, although most specimens can be assigned to one or the other species with reasonable confidence.

The type material of *Rissoa perforata* Thiele, 1925 conforms to *Lucidestea* as defined by Ponder (1985b) and, consequently, *L. perforata* Laseron is a secondary homonym. The replacement name is named for Charles Laseron (1887-1959) who contributed an enormous amount to the understanding of small Australian molluscs.

Calopia minutissima n. sp.
(Figs 2D,E, 3C-E, 5D, 8D,E, 10E,F, 11D,F-H, 12B, 13, 14)

Type material: Holotype (Fig. 11D) AMS, C 337878.
Paratypes AMS, C 330800 (many), NTM (4). Nightcliff, Darwin, 12°23'S, 130°50'E, W.F.Ponder, 15 July 1988. In short algae, on intertidal flats.

Other material examined (all AMS):
Northern Territory. Buchanan Is, S side of Melville Is, 11°49'S, 130°39'E, N.Kamper, 2 Dec. 1938, C 327445 (4), C 327301 (2); Fannie Bay, Darwin, 12°26'S, 130°49'E, W.F.P., 14 Jul.1988, C 330802 (4); Nightcliff, Darwin, 12°23'S, 130°50'E, W.F.P., 15 Jul. 1988, C 330804 (24), C 328442 (10), C 328441 (many), C 328440 (4), C 328446 (many), C 328445 (12), C 330798 (9); C 328263 (many); Port Darwin, 12°28'S, 130°50'E, J.Laseron, circa 1940, C 328221 (1), C 322942 (11); East Arm, Darwin, 12°30'S, 130°55'E, W.F.P., 16 Jul. 1988, C 328444 (9), C 328443 (8).
Queensland. ca. 2 miles off Horsey R. mouth, Gulf of Carpentaria, 14°35'S, 141°30'E, C.Hedley, 3 Jun. 1903, C 15135 (2); Beaches around Mapoon, Gulf of Carpenteria, 11°58'S, 141°53'E, C.Hedley, 23 May 1903, C 328409 (9); Somerset Bay, Cape York Peninsula, 10°44.5'S, 142°35.5'E, W.F.P. & I.Loch, 10 Jul. 1976, C 327173 (26), C 328405 (many); S side of Fly Point, Somerset, 10°45'S, 142°36'E, W.F.P. & I.Loch, 11 Jul. 1976, C 327430 (3), C 327152 (1); Lindeman Is, 20°27'S, 149°2'E, M. Ward, 3 Mar. 1934, C 327442 (3); Facing Is, Port Curtis, 23°49'S, 151°22'E, pre 1967, C 328406 (many); Tannum Sands, Port Curtis, 23°57'S, 151°22'E, B.Page, 1969, C 327192 (1); Dundowran Beach, Hervey Bay, 25°18'S, 152°6'E, B.Page, C 316555 (2).

Diagnosis: Shell small for genus (up to 0.96 mm in length), ovate, broadly umbilicate. Penis with two apocrine glands and no basal lobe.

Description:
Shell (Fig. 11A-C, E): Minute (up to 0.96 mm in length), ovate, smooth, of up to 3.75 (usually less than 3.5) weakly convex whorls. Aperture mainly separated from parietal wall, sub-pyriform, angled posteriorly, rounded anteriorly. Base convex, with wide, open umbilicus occupying about 19-21% of width of base (also very widely open in juveniles) and sculptured with prominent axial rugae. Base sculptured with few spiral ridges on lower half of base, one ridge more prominent than rest bordering umbilicus and, usually, two on lower base. Peristome thin, simple. Periostracum thin, transparent, shell white.

Operculum (Fig. 2D,E): Subcircular, as for genus.

Head-foot (Fig. 5D, 8D): Mainly translucent white; snout with dense-white pigment dorsally, and, in some specimens, with some lateral black pigment. Eyes in weak bulges at base of tentacles, with pale orange `eyebrow'. Left tentacle with two ciliated bulges on posterior part of outer edge, inner edges of both tentacles and latero-ventral edges with short, actively beating cilia. Long compound cilia (`setae') distally on both tentacles. Tentacles with dense-white spots and a narrow black spot at about anterior third on lateral edges of both tentacles (i.e., not a complete band). Sides of neck and anterior opercular lobe grey to black, although interrupted by a narrow unpigmented strip down both sides of neck. Anterior margin of foot ciliated, indented, laterally expanded, with propodium across entire edge. Anterior mucous gland extends almost entire width of foot as a narrow gland but longer in middle. Mantle (as seen through shell) variable in colour but mostly whitish with small irregular

brown markings. Posterior end of foot unpigmented, narrowly rounded, with short, setose metapodial tentacle at posterior end. Pallial edge simple, ciliated.

Table 5
Shell dimensions of *Calopia minutissima* n.sp.

	SL	SW	AL	AW	WH
Holotype	0.99	0.97	0.52	0.45	3.90
Figured specimens					
Paratype (immature)	0.58	0.61	0.38	0.34	3.00
Cape York, Qld, AMS, C 328405	0.85	0.82	0.43	0.36	3.10
Nightcliff, Darwin, NT. AMS, C 330800. Paratypes (n=20)					
Min	0.64	0.66	0.35	0.32	2.80
Max	0.89	0.85	0.45	0.40	3.45
Mean	0.757	0.746	0.407	0.358	3.145
SD	0.075	0.056	0.029	0.021	0.186
Port Darwin, NT. AMS, C 322942 (ex Laseron, with topotypes of *C. laseroni*)(n=4)					
Min	0.84	0.86	0.47	0.40	3.50
Max	0.96	0.88	0.49	0.42	3.70
Mean	0.902	0.867	0.477	0.410	3.600
SD	0.049	0.010	0.010	0.012	0.082
East Point Darwin, NT. (together with *C. laseroni*) AMS, C 339297(n=2)					
Min	0.69	0.71	0.40	0.35	2.10
Max	0.74	0.75	0.41	0.41	2.70
Mean	0.715	0.730	0.405	0.380	2.400
SD	0.035	0.028	0.007	0.042	0.424
Cape York, Qld. AMS, C 328405 (n=9)					
Min	0.71	0.70	0.39	0.32	3.25
Max	0.96	0.85	0.52	0.46	3.75
Mean	0.842	0.788	0.477	0.399	3.472
SD	0.082	0.052	0.045	0.038	0.200
Mapoon, Qld. AMS, C 328409	0.87	0.77	0.44	0.40	3.25
Facing Is, Port Curtis, Qld. AMS C 328406	0.79	0.73	0.45	0.38	3.30

Radula (Fig. C-E): As for genus. Central 2+1+2, median cusp narrow, sharp; lateral teeth 2+1+4, median cusp pointed; cusps on inner and outer marginal teeth unable to be counted accurately.

Penis (Figs 8D,E, 10E,F): with one large, long apocrine gland on inner side, a single smaller, narrow gland behind; no basal glandular lobe. Base thick and short.

Distribution (Fig. 13): Darwin area, eastern Gulf of Carpentaria, Cape York and tropical east Queensland coast.

Remarks: This species is similar to *C. laseroni* and *C. burni* in its ovate shell shape and wide umbilicus but differs from the species described above in its smaller size and wider umbilicus. It differs from the sympatric *C. laseroni* in having prominent spiral ridges/grooves surrounding the umbilicus (the spiral ridge bordering the umbilicus is stronger than the rest) and in the umbilicus being more open, the sides being more visible and clearly sculptured with axial rugae. In *C. laseroni* the umbilicus is bordered by a prominent ridge which is usually angular, rarely a narrow ridge, and other basal sculpture is typically weak. The umbilicus in *C. laseroni* is also relatively narrower, with steeper sides and the axial growth lines are usually not readily observed because of the steep sides and are usually not developed into prominent rugae.

In head-foot characters *C. minutissima* differs from *C. imitata* in having relatively shorter cephalic tentacles that lack black pigment at their bases and in the lack of pigment on the foot (with the exception of the opercular lobe) (Note: the living animal of *C. burni* was not examined in sufficient detail for comparison and that of *C. laseroni* has not been examined). *Calopia minutissima* has a more nearly circular operculum than thE species described above, but this is a paedomorphic feature, juvenile specimens of the larger species also having a near circular operculum.

Juveniles of this species have a widely open umbilicus whereas in *C. imitata* and *C. burni* the umbilicus is narrow in juveniles, broadening in adults of *C. burni*. In *C. laseroni* the umbilicus remains moderately open throughout growth but is relatively narrower and steeper sided than in *C. minutissima*.

Some specimens from north Queensland are similar in shell characters to this species and are tentatively assigned to it. Assuming that these identifications are correct, the species has an extensive range in northern Australia. However, there is inadequate material to determine whether or not the penial characters are similar throughout this range, as nearly all the available material is empty shells.

This species appears to be sympatric with *C. laseroni* over all of its range. A few of the latter species were obtained on the intertidal flats at Nightcliff, but only as empty shells, suggesting that the two species occupy largely different habitats.

Comparison of Shell Morphology:
All species are very similar in shell morphology. With pooled data, reasonably

good separation can be achieved with shell size and shape parameters (see Fig. 14). *Calopia minutissima* and *C. laseroni* are significantly different from each other and *C. imitata* and *C. burni* in shell length, width and aperture length and width (all P<0.001 [1]). However, *C. imitata* and *C. burni* are not significantly different in any of these shell measurements (P=0.037, P=0.077, 0.557 and 1.000 respectively). However, when the ratios of these measurements were compared, *C. imitata* and *C. burni* are significantly different in shell width/shell length and aperture length/shell length (P<0.001) as are the other comparisons except for *C. burni* and *C. laseroni* (P=0.166 and 1.000 respectively). The number of whorls differed between species, with most comparisons being highly significant (P<0.001; *C. imitata* and *C. burni* P=0.005), but with no significant difference between *C. burni* and *C. laseroni* (P=0.023).

As might be expected from these results, a discriminant function analysis failed to classify more than 82% of specimens in their `correct' species. These results may indicate incorrect initial assignment in some cases, particularly with the Queensland material.

Table 6

Classification matrix (cases in row categories classified into columns) from discriminant function analysis using shell length and width and aperture length and width measurements.

	imitata	*minutissima*	*burni*	*laseroni*	% correct
C. imitata	26	0	5	3	**76**
C. minutissima	0	28	0	9	**76**
C. burni	1	0	19	0	**95**
C. laseroni	0	7	0	38	**84**
Total	27	35	24	50	**82**

Phylogenetic Relationships

Calopidae is a member of a group of rissooidean families (including Hydrobiidae, Pomatiopsidae, Stenothyridae, Vitrinellidae, Assimineidae, Hydrococcidae, Truncatellidae and Iravadiidae) that have pallial gonoducts with complex histology (Ponder, 1988). The present analysis shows a somewhat different (but poorly supported) topology to that obtained in my earlier analysis. A molecular data set of many of these taxa is currently being analysed and will hopefully assist in resolving the relationships of these taxa.

A maximum parsimony analysis using the data matrix in Table 7 was undertaken. Of the 57 characters used, 8 (characters 1, 11, 20, 26, 38, 41, 43 and 55) were phylogenetically uninformative and were excluded. The analysis produced 40 trees 152 steps long (CI 0.408, RI 0.0.508, RC 0.207, HI 0.592). The strict consensus (Fig. 15A) and majority rule (Fig. 15B) trees are illustrated. While the results are not particularly clear-cut, it appears that *Calopia* may be most closely related to the Hydrobiidae (*sensu lato*) although this relationship has no bootstrap support (100 replications, each with 5 random subreplications with 5 trees held at each step). The bootstrap retained a clade containing all non-rissoid taxa, and a single subclade (*Caecum* + *Circulus*).

1 Calculated using analysis of variance with a Bonferroni adjusted *post hoc* test.

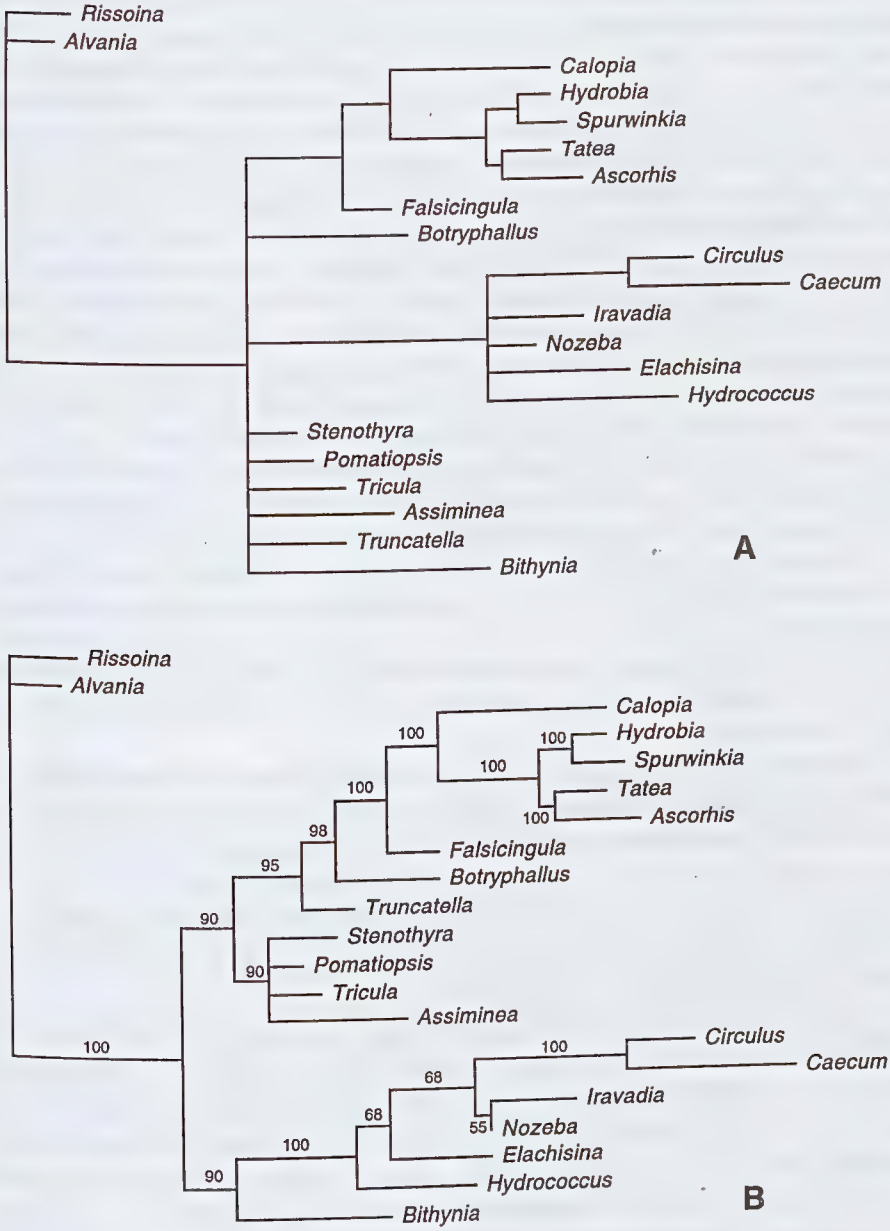

Figure 15.
Phylogram of strict (A) and majority rule (B) consensus trees (see text for details) based on the morphological data in Table 7. The numbers at the nodes in B are the percentages (>50%) of trees supporting that node.

In the maximum parsimony analysis the clade containing *Calopia* and the Hydrobiidae is sister to *Falsicingula*. This clade is poorly supported by spiral sculpture on protoconch I (a highly homoplastic character), and two unlikely reversals - a reduced to well developed ctenidium and a short to long osphradium.

Using the unmodified data set, three characters are apomorphies of the clade *Calopia* (Hydrobiidae); protoconch II absent to present (an unlikely reversal), cephalic tentacles with a black band and right cephalic tentacle with ciliated rugae on its base. The latter two characters, while possibly plesiomorphic within hydrobiids, have been lost in the majority of taxa. *Calopia* is set off from the hydrobiids by eight apomorphies (compound cilia, metapodial tentacle, calcareous operculum, intestine loops in middle of style sac, right S-shaped coiled intestine, few, large testis lobes, apocrine glands (also in many cochliopine hydrobiids) and egg capsules in a row, although the last character is also seen in some cochliopine hydrobiids not included in the analysis (see Hershler & Ponder, 1998 for references). The hydrobiid clade is supported by a shorter osphradium, spirals on protoconch II (a very inconstant character), a neck separating the cutting edge and the shaft on the lateral teeth, a coiled renal oviduct and a clearly differentiated albumen gland.

Although *Calopia* has a swimming veliger, there is no division into a distinct protoconch I and II suggesting that development is lecithotrophic and that dispersal may be hindered by a relatively short planktonic life.

The new family differs from other rissooidean families in possessing the combination of characters outlined in the diagnosis, of which the following are apomorphies:-

Metapodial tentacle at the posterior end of the foot. This character is also seen in some vitrinellids, a few iravadiids, all(?) stenothyrids and *Elachisina*, but never in hydrobiids.

Propodium located behind the anterior edge of the foot. Typically located at the anterior edge of the foot and extends across the whole anterior margin. A somewhat similar, and presumably convergent, placement of the propodium is seen in some assimineids (e.g. Fukuda & Mitoki, 1996, fig. 42).

Long compound cilia (`setae') on the distal ends of the cephalic tentacles. Also seen in vitrinellids and caecids but not in hydrobiids, bithyniids, stenothyrids, truncatellids or assimineids.

Poorly developed ctenidial filaments lacking skeletal rods. The plesiomorphic state for all caenogastropods is the possession of skeletal rods (Haszprunar, 1988; Ponder & Lindberg, 1997), therefore their loss in *Calopia* is certainly secondary, possibly due to the reduction in size of the filaments. The secondary loss of the skeletal rods is also seen in some other small caenogastropods, including hydrobiids (R. Hershler, pers.comm.).

Strongly S-shaped looped intestine. Most rissooideans have `straight' intestines (i.e., that follow the curvature of the right side of the pallial cavity), although S-shaped looped intestines are also found in some hydrobiids (e.g. Hershler & Longley, 1986; Ponder, 1992; Ponder *et al.*, 1993) and caecids (Götze, 1938; Marcus & Marcus, 1963). Hershler & Ponder (1998) point out that the looping can occur in two different directions. In *Calopia* it coils to the right, the same direction as in *Pseudotricula eberhardi* Ponder (Ponder, 1992).

Intestine looped around the middle of the style sac. This state is also seen in *Elachisina* (Elachisinidae, Ponder, 1985a) and at least some Vitrinellidae. In most rissooideans (and other caenogastropods) the intestine is looped around

the anterior end of the style sac, although the distribution of the apomorphic state is not well understood because the relationship of the intestine and the style sac are often not described.

Posteriorly located bursa copulatrix. This apomorphy is shared with Rissoidae, Hydrobiidae, Assimineidae, Stenothyridae and Pomatiopsidae. Some families (Iravadiidae, Elachisinidae, Vitrinellidae, Bithyniidae) have anteriorly located bursae. The bursa in *Hydrococcus* is in part anterior but its homology is uncertain (as reflected in the scoring in Table 7). Some rissoids (e.g. *Lucidestea* and *Rissoina*) have anterior sperm sacs that function as bursae but also have a posterior bursa (Ponder, 1985b). The uncertainty of the homology of the anterior sperm sac in *Rissoina* is reflected in the scoring in Table 7. The female reproductive system of *Calopia* is one of the simplest yet described in the superfamily. The lack of a seminal receptacle is probably secondary and the function of that structure has apparently been taken over by the bursa copulatrix, which has both unoriented and oriented sperm and a short duct. The uniform oviduct gland is also unusual in rissooideans (see Table 7, character 46), and its position entirely within the pallial cavity is also unusual, especially amongst the hydrobioids.

Penial apocrine glands. Similar glands are found in many Cochliopinae (Hydrobiidae) (Hershler & Thompson, 1992), and some iravadiids (Ponder, 1984; Fukuda *et al.*, 1990), caecids (Marcus & Marcus, 1963), and a few pomatiopsids (e.g. Abbott & Hunter, 1949) and some vitrinellids (WFP, pers. observ.).

Egg capsules in rows. Double rows of capsules are seen in bithyniids (e.g. Fretter & Graham, 1962, fig. 207) and some cochliopines produce a single row of capsules but otherwise rissooideans, with few exceptions (see Hershler & Ponder, 1998) produce single capsules.

No separate seminal receptacle. The seminal receptacle is absent in a few taxa in several other groups but this state is unlikely to be plesiomorphic as the presence of a seminal receptacle derived from the renal oviduct is one of the characters that define the Sorbeoconcha (Ponder & Lindberg, 1997). In *Calopia* the function of the seminal receptacle is presumably taken over by the bursa as orientated sperm is found in part of that structure.

The lack of a well-developed renal oviduct is probably plesiomorphic and is shared with the Vitrinellidae, Elachisinidae and Caecidae. A renal oviduct is weakly developed in the Iravadiidae and well developed in Bithyniidae, Hydrobiidae, Pomatiopsidae and Assimineidae. In the Rissoidae the posterior gland of the oviduct is thought to be homologous with the renal oviduct (Ponder, 1985b), although this supposition requires testing.

Some of the important characters distinguishing related taxa from Calopiidae are summarised below.

Rissoidae. The members of this large, diverse family differ from *Calopia* in having a glandular renal oviduct, and in lacking a metapodial tentacle on the posterior end of the foot, although some have one or three doubtfully homologous tentacles emerging from beneath the operculum (Ponder, 1985b).

Bithyniidae. Similar in having calcareous material in the operculum, and in general teleoconch morphology. It differs in several characters, including having

a large accessory lobe on the penis with an internal gland extending into the cephalic haemocoel, no apocrine glands, and the oviduct has an anterior bursa copulatrix and a well-developed renal oviduct. There are no compound cilia on the cephalic tentacles, the mantle edge has a `siphon' on the right side - a modification related to the filter feeding habit of the family, and the foot lacks a metapodial tentacle.

Iravadiidae. The protoconch is smooth and flattened and the operculum lacks calcareous material. There are no compound cilia on the cephalic tentacles and no metapodial tentacle in most taxa. The female reproductive system has an anterior bursa copulatrix.

Stenothyridae. There are no compound cilia on cephalic tentacles and the operculum has two characteristic pegs and lacks calcareous material. The radula has multiple basal cusps on the central teeth. The male reproductive system differs in having a simple penis, while the female has a very different reproductive system with a posterior sperm duct opening and a well-developed renal oviduct.

Assimineidae. There are no compound cilia on the cephalic tentacles and no metapodial tentacle. The male reproductive system differs in having a simple penis and the female has a well-developed renal oviduct and a seminal receptacle. The radula has multiple basal cusps and the head foot is modified (in Assimineinae) with very short tentacles and an omniphoric groove.

Hydrobiidae. There are no compound cilia on the cephalic tentacles and no metapodial tentacle. The osphradium is short, usually less than half the length of the ctenidium. Penial apocrine glands are found only in Cochliopinae (Hershler & Thompson, 1992). There is a great deal of diversity in the male and female reproductive systems, although most taxa have a seminal receptacle (or rarely two or more). There can be either a ventral channel or a separate sperm tube in the oviduct and all have a well-developed renal oviduct.

Pomatiopsidae. There are no compound cilia on the cephalic tentacles and no metapodial tentacle. The penis is simple and there is a separate sperm tube in the female (the ventral channel is absent), and there is a well-developed renal oviduct.

Hydrococcidae. There are no compound cilia on the cephalic tentacles and no metapodial tentacle. A long, double pallial tentacle is present. The circular operculum lacks calcareous material. The female reproductive system differs in many characters.

Falsicingulidae. There are no compound cilia on the cephalic tentacles and no metapodial tentacle. The operculum is horny and the penis simple. The radula has two pairs of basal denticles, the kidney and/or pericardium is modified to store sperm and the pallial oviduct lacks a ventral channel.

Elachisinidae. This family shares a few features with Calopiidae, including having a metapodial tentacle. The foot is distinctly cleft posteriorly and, as in *Calopia,* the intestine passes around the middle of the style sac. *Elachisina* also has a similarly shaped prostate gland that differs in being ventrally open. *Elachisina* lacks large apocrine glands on the penis, although smaller, simple glands are present. The female reproductive system differs in having a pallial bursa and distinct capsule and albumen glands. *Elachisina* also differs from

Calopia in having a simple, horny, oval operculum, a pair of pallial tentacles, a well-developed renal oviduct and two seminal receptacles.

Vitrinellidae. Members of this family have flattened shells and a circular operculum. The female reproductive system differs in several details, such as having a posterior pallial opening, and an anterior bursa copulatrix. A ventral ring of cilia on the antero-ventral surface of the cephalic tentacles of at least some vitrinellids (Bieler & Mikkelsen, 1988; Ponder, 1994) may be a useful synapomorphic character for this family but insufficient information is available about this character within the vitrinellids and its presence in other presumably related taxa such as the Iravadiidae. This ring of cilia is not present in *Calopia*. Similarities with *Calopia* include a posterior metapodial tentacle and apocrine glands, both of which are found in only some vitrinellids.

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Table 7
Data matrix used in the maximum parsimony analysis. Characters are listed in Table 8 and the sources of information and family designations are given in Table 9. Uninformative characters are indicated by an asterisk and were excluded from the analysis.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Uninformative	*										*				
Rissoina	0	1	1	0	0	0	?	0	0	0	0	0	1	1	1
Alvania	0	1	1	0	0/1	0/1	0/1	0	0	0	0	0	1	0	1
Calopia	0/3	0/1	0	0	1	0	0	0	1	1	0	1	0	-	0
Hydrobia	0	0	0	0	0	0	0/1	0	0/1	0	0	1	1	0	0
Tatea	0	0	0	0	0	0	1	0	1	0	0	1	0	-	0
Spurwinkia	0	0/1	0	0	1	0	1	0	1	0	0	1	0	-	0
Botryphallus	0	0	0	0	0	1	-	0	0	0	?	?	0	-	0
Circulus	1	1	0	1	0	0	0	0	0	1	1	?	1	1	0
Falsicingula	0	0	0	0	1	1	-	0	0	0	0	0	0	-	0
Stenothyra	0	1	0	0	0	1	-	0	0/1	0	0	0	0	-	0
Iravadia	0	1	0/1	1	0	0	0	0	1	0	?	0	0	-	0
Nozeba	0	0/1	0	1	0	0	0	0	0	0	?	0	1	0	0
Elachisina	0/3	1	0	0	0	1	0	0	0	0	?	0	1	1	1
Pomatiopsis	0	0	0/1	0	0	1	-	1	0	0	0	0	0	0	0
Tricula	0	0	0	0	0	1	-	0	0	0	0	0	0	0	0
Assiminea	0/3	0/1	0	0	0	1	-	2	0	0	0	0	0	0	0
Hydrococcus	0/3	0	0	0	0	1	-	0	0	0	?	0	1	1	0
Caecum	2	0/1	0/1	1	0	0	0	0	0	1	?	1	0	-	0
Truncatella	0	0	1	0	0	1	-	1	0	0	0	0	0	-	0
Bithynia	3	0/1	0/1	0	0	1	-	0	0	0	0	0	0	-	0
Ascorhis	0	1	0	0	1	0	-	0	1	0	0	1	0	-	0

Character	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Uninformative					*						*				
Rissoina	0	0	0	0	-	1	1	1	0	0	1	1/2	2	1	0
Alvania	0	0	0	0	0	1	1	1	0	0	1	0	2	1	0
Calopia	0/1	0/1	1	1	0	0/1	1	1	0	0	1	0	1	0	1
Hydrobia	0	0	0	0	-	1	1	1	0	2	1	0	1	0	1
Tatea	0	0	0	1	1	1	1	1	0	2	1	2	1	0	1
Spurwinkia	0	1	0	0	-	1	1	1	0	2	1	0/1	1	0	1
Botryphallus	0	0	0	0	-	1	1	1	1	1	1	0	1	1	1
Circulus	1	1	0	0	-	0	0	0	0	1	1	1	2	1	0
Falsicingula	0	0	0	0	-	1	1	1	0	0	1	1	1	0	1
Stenothyra	0	0	1	0	-	1	1	1	0	1	1	2	1	0	1
Iravadia	0/1	1	0/1	0	-	1	1	2	0	1	0/1	0/1	1	0	1
Nozeba	0	1	0	0	-	1	1	1	0	1	1	1	2	1	1
Elachisina	1	1	1	0	-	1	1	1	0	2	1	1	2	1	1
Pomatiopsis	0	0	0	0	-	1	1	1	0	1/2	1	1/2	1	0	0
Tricula	0	0	0	0	-	1	1	1	0	2	1	1/2	1	0	0
Assiminea	0	0	0	0	-	1	1	1	1	2	1	2	1	0	1
Hydrococcus	0	1	0	0	-	0	0	0	1	2	1	1	2	1	1
Caecum	0	0	0	0	-	0	0	0	0	0	0	-	2	0	0
Truncatella	0	0	0	0	-	1	1	1	1	1	1	2	0	0	0
Bithynia	0	0	0	1	0	1	2	1	0	2	1	2	2	2	0
Ascorhis	0	0	0	0	-	1	1	1	0	2	1	0	2	0	1

Character	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Uninformative								*			*		*		
Rissoina	0	0	0	0	0	0	0	0	0	2	1	?	?	1	0
Alvania	0	0	1	0	1	0	0	0	0	2	1	0	-	1	0
Calopia	0	2	1	0	0	1	1	0	1	0	0	0	-	1	1
Hydrobia	1	2	1	0	0	0	0	0	1	1	1	0	-	1	1
Tatea	1	2	1	0	0	0	0	0	0	1	1	0	-	1	1
Spurwinkia	1	2	1	0	0	0	0	0	1	1	1	0	-	1	1
Botryphallus	1	2	1	0	0	?	0	0	?	0	1	1	0	0	0
Circulus	0	0	?	0	0	1	0	0	?	1	1	1	0	0	1
Falsicingula	0	2	1	0	1	0	0	0	?	0	1	0	-	1	1
Stenothyra	0	2	1	0	0	0	0	0	1	1	1	0	-	1	1
Iravadia	0	2	1	0	0	?	0	0	?	0	1	1	0	0	1
Nozeba	0	2	1	0	0	?	0	0	?	0	1	1	0	0	1
Elachisina	1	2	1	0	0	1	1	0	0	1	1	1	1	0	1
Pomatiopsis	0	0/2	0/1	0	0	0	0	0	1	1	1	0	-	1	1
Tricula	0	0	0	1	0	0	0	0	1	1	1	0	-	1	1
Assiminea	1	?	?	1	1	0	0	0	1	1	1	0	-	1	1
Hydrococcus	0	?	1	0	0	1	0	0	0	1	?	?	?	?	1
Caecum	0	2	2	0	1	?	3	0	?	0	1	1	0	0	0
Truncatella	0	2	1	0	0	0	0	0	?	0	1	0	-	1	1
Bithynia	0/1	2	0	1	0	0	0	1	0/1	1	1	1	0	0	1
Ascorhis	1	2	1	0	1	0	0	0	0	1	0/1	0	-	1	1

Character	46	47	48	49	50	51	52	53	54	55	56	57
Uninformative										*		
Rissoina	?	1	1	0	0	1	1	0	0	0	0	1
Alvania	1	1	1	0	0	0	0/1	1	0	0	0	1
Calopia	0	1	1	2	1	0	0	0	1	1	0	0
Hydrobia	1	1	1	1	0	0	1	0	0	0	0	0
Tatea	1	1	1	0	0	0	0	0	0	0	0	0
Spurwinkia	1	2	1	1	0/1	0/1	1	0	1	0	0	0
Botryphallus	0	1	1	?	1	0	0	0	?	?	0	0
Circulus	0/1	1	2	?	0/1	0	0	0	0	0	0	0
Falsicingula	0	2	1	0	0	0	0	0	0	0	0	0
Stenothyra	1	2	1	1	0	0	0	0	?	0	0	0
Iravadia	1	0/1	?	?	0/1	0/1	0/1	0	?	0	0	0
Nozeba	?	1	2	?	0	1	0	0	?	0	0	0
Elachisina	1	1	1	1	0	1	0	0	?	0	0	0
Pomatiopsis	1	2	1	1	0	0	0	0	0	0	1	0
Tricula	1	2	1	1	0	0	0	0	0	0	0	0
Assiminea	1	2	1	2	0	0	0	0	0/2	0	1	0
Hydrococcus	1	2	1	0	0	1	1	0	1	0	0	0
Caecum	1	?	1	1	1	1	0	0	0	0	0	0
Truncatella	?	1	1	?	0	0	0	0	?	0	?	0
Bithynia	1	1	1	0	0	0	0	1	2	0	0	0
Ascorhis	1	0	1	0	0	0	0	1	?	?	?	0

Table 8
List of characters used in the analysis and description of their states.

1. *Shell shape.* 0 - conical to elongate, 1 - flattened, 2 - tube-like (uninformative).
2. *Spiral sculpture.* 0 - absent, 1 - present.
3. *Axial sculpture.* 0 - absent, 1 - present.
4. *Protoconch shape.* 0 - conical to dome-shaped, 1 - planorboid.
5. *Protoconch I spiral sculpture.* 0 - absent, 1 - present.
6. *Protoconch II.* 0 - present, 1 - absent.
7. *Protoconch II microsculpture, spirals.* - inapplicable, 0 - absent, 1 - present.
8. *Cephalic tentacle shape.* 0 - long, slender, 1 - short, stubby, 2 - very short.
9. *Cephalic tentacle pigment.* 0 - without black band, 1 - with black band.
10. *Cephalic tentacles with long `setae' (compound cilia) distally.* 0 - absent, 1 - present.
11. *Cephalic tentacles with circular pad antero-ventrally.* 0 - absent, 1 - present (uninformative - due to large amount of missing data).
12. *Right cephalic tentacle with ciliated rugae at base.* 0 - absent, 1 - present.
13. *Posterior pallial tentacle.* 0 - absent, 1 - present.
14. *Number of posterior pallial tentacles.* - inapplicable, 0 - one, 1 - two.
15. *Anterior pallial tentacle.* 0 - absent, 1 - present.
16. *Posterior end of foot.* 0 - rounded, 1 - indented.
17. *Anterior end of foot.* 0 - flat or evenly convex, 1 - indented.
18. *Metapodial tentacle at posterior end of foot.* 0 - absent, 1 - present.
19. *Operculum - structure.* 0 - horny, 1 - calcareous (white).
20. *Operculum - calcareous (white) material.* - inapplicable, 0 - incorporated in body of operculum, 1 - smear and/or pegs on inner side (uninformative).
21. *Operculum - shape.* 0 - circular, 1 - oval.
22. *Operculum - coiling I.* 0 - multispiral, 1 - paucispiral, 2 - concentric.
23. *Operculum - nucleus.* 0 - central, 1 - eccentric, 2 - marginal.
24. *Ctenidium.* 0 - well developed, 1 - reduced or absent.
25. *Osphradium.* 0 - long (longer than half length of ctenidium), 1 - medium (about third to half length of ctenidium), 2 - short (shorter than a third of length of ctenidium).
26. *Basal denticles on central teeth.* 0 - absent, 1 - present (uninformative).
27. *Number of basal denticles on central teeth.* - inapplicable, 0 - one, 1 - two, 2 - more than two.
28. *Lateral teeth outer flanks.* 0 - shorter to about equal to cutting edge, 1 - a little longer to about twice width of cutting edge, 2 - much longer than cutting edge.
29. *Denticle on face of lateral teeth.* 0 - absent, 1 - present.
30. *Basal projection on lateral teeth.* 0 - absent, 1 - present.
31. *Neck separating cutting edge from shaft on lateral teeth.* 0 - absent, 1 - present.
32. *Inner marginal teeth.* 0 - denticles on both sides, 1 - denticles on inner side, 2 - denticles on outer side.
33. *Outer marginal teeth.* 0 - denticles on both sides, 1 - denticles on inner side, 2 - denticles on outer side.
34. *Outer marginal distal end.* 0 - narrow, pointed, 1 - narrow, rounded, 2 - broad.
35. *Cusps on marginal teeth.* 0 - equal to subequal in size, 1 - markedly larger on inner marginal.
36. *Intestinal loop around style sac.* 0 - at anterior end, 1 - in middle.
37. *Intestine in pallial cavity.* 0 - straight or with simple loop, 1 - S-shaped coil to right, 2 - S-shaped coil to left, 3 - double S-shaped coil.
38. *Kidney.* 0 - confined to visceral mass or extending into posterior mantle roof, 1 - extending into anterior mantle roof (uninformative).
39. *Ovary.* 0 - simple, 1 - distinctly lobulate.

40. *Renal oviduct.* 0 - short, simple, 1 - coiled, 2 - glandular.
41. *Seminal receptacle from renal oviduct.* 0 - absent, 1 - present (uninformative).
42. *Anterior bursa copulatrix.* 0 - absent, 1 - present.
43. *Anterior bursa opening.* - inapplicable, 0 - anterior, 1 - posterior (uninformative).
44. *Posterior bursa copulatrix.* 0 - absent, 1 - present.
45. *Oviduct gland histology.* 0 - simple, 1 - complex.
46. *Albumen gland and capsule gland.* 0 - not clearly differentiated, 1 - clearly differentiated.
47. *Ventral wall of pallial oviduct.* 0 - open, 1 - closed, thin, forming ventral channel, 2 - thick and glandular.
48. *Position of female pallial opening.* 0 - ventrally open, 1 - open anteriorly, 2 - open posteriorly.
49. *Testis.* 0 - simple acini, 1 - lobules, 2 - few large lobes.
50. *Penis - apocrine glands.* 0 - absent, 1 - present.
51. *Penial glands (excluding apocrine glands).* 0 - absent, 1 - present.
52. *Non-glandular penial lobes.* 0 - absent, 1 - present.
53. *Penis - internal glands.* 0 - absent, 1 - present.
54. *Egg capsules.* 0 - single, 1 - in chain, 2 - in cluster.
55. *Propodium.* 0 - at anterior edge, 1 - behind anterior edge (uninformative).
56. *Omniphoric groove.* 0 - absent, 1 - present.

Table 9
Published sources of information for taxa used in the cladistic analysis.

Rissoina and *Alvania* (Rissoidae). Ponder, 1968, 1985b; Sleurs, 1993.
Hydrobia (Hydrobiidae). Fretter & Graham, 1962; Hershler & Davis, 1980; Davis *et al.*, 1988b, 1989.
Tatea (Hydrobiidae). Ponder *et al.*, 1991.
Spurwinkia Littoridina, Heleobops etc. (also includes) (Cochliopinae, Hydrobiidae). Marcus & Marcus, 1963; Davis *et al.*, 1982, 1988b; Davis & McKee, 1989; Hershler & Thompson, 1992.
Botryphallus (family uncertain, tentatively Hydrobiidae). Ponder, 1990.
Circulus (Vitrinellidae). Fretter, 1956; Bieler & Mikkelsen, 1988; Ponder, 1994.
Falsicingula (Falsicingulidae). Slavoshevskaya, 1975, 1982; Ponder, 1985b.
Stenothyra (Stenothyridae). Kosuge, 1969; Davis *et al.*, 1986a, 1988a.
Iravadia (Iravadiidae). Ponder, 1984; Fukuda *et al.*, 1990.
Nozeba (Iravadiidae). Ponder, 1984.
Elachisina (Elachisinidae). Ponder, 1985a.
Pomatiopsis (Pomatiopsidae). Dundee, 1957; Davis, 1967.
Tricula (Pomatiopsidae). Davis *et al.*, 1986b, c.
Assiminea (Assimineidae). Hershler, 1987.
Hydrococcus (Hydrococcidae). Ponder, 1982.
Caecum (Caecidae). Götze, 1938; Marcus & Marcus, 1963.
Truncatella (Truncatellidae) Vayssière, 1885; Fretter & Graham, 1962; Kosuge, 1966.
Bithynia (Bithyniidae). Seshaiya, 1930; Schäfer, 1952; Lilly, 1953; Fretter & Graham, 1962; Itagaki, 1965; Chung, 1984; Chitramvong, 1991

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A comparison of two onchidiid species (Mollusca, Pulmonata)

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Abstract

Two externally similar species of Onchidiidae (Superfamily Onchidioidea), *Onchidium verruculatum* and *Onchidina australis*, occur together at Careel Bay in Sydney, NSW. These species were identified in a study of both external and internal morphology. The alimentary system and reproductive structures were examined and are illustrated. The most obvious external character separating the two species is the position of the pneumostome, which is located posteriorly in the midline in *Onchidium verruculatum* and to the right of the midline in *Onchidina australis*. In addition, differences in shape and colour distinguish the two species, as does presence or absence of accessory eyes. Important anatomical differences are the length of the penis and the presence or absence of an accessory penial gland, the number of lobes of the ovotestis and the presence or absence of a crop.

Key words: Onchidiidae, Australia

Introduction

The Onchidioidea is a group of marine pulmonate molluscs containing one family, Onchidiidae. For a recent summary of the group in Australia see Stanisic (1998). This family has been considered taxonomically difficult because few of the external characters can be used to distinguish between genera and species, especially if only preserved material is available.

Members of this group are slug-like and are usually found between tide marks, in holes and burrows or under logs and rocks. Onchidiids are found in tropical and continental areas, usually in mangrove swamps or estuarine shores, and less commonly on rocky shores. The highest diversity is in Southeast Asia (Britton, 1984). Five species have previously been recorded from around Sydney (Bretnall, 1919; Dakin, 1947): *Onchidium verruculatum* Cuvier 1830, *Onchidium damelli* Semper 1882, *Onchidella patelloides* Quoy and Gaimard 1832, *Onchidina australis* Semper 1882 and *Platevindex chameleon* Brazier 1886. The onchidiids of New South Wales or, indeed, Australia have not been reviewed since Bretnall's (1919) study. Smith and Kershaw (1979) provide a key to the South East Australian species. The reader is referred to Bretnall (1919) for details of the available names and original taxonomic references.

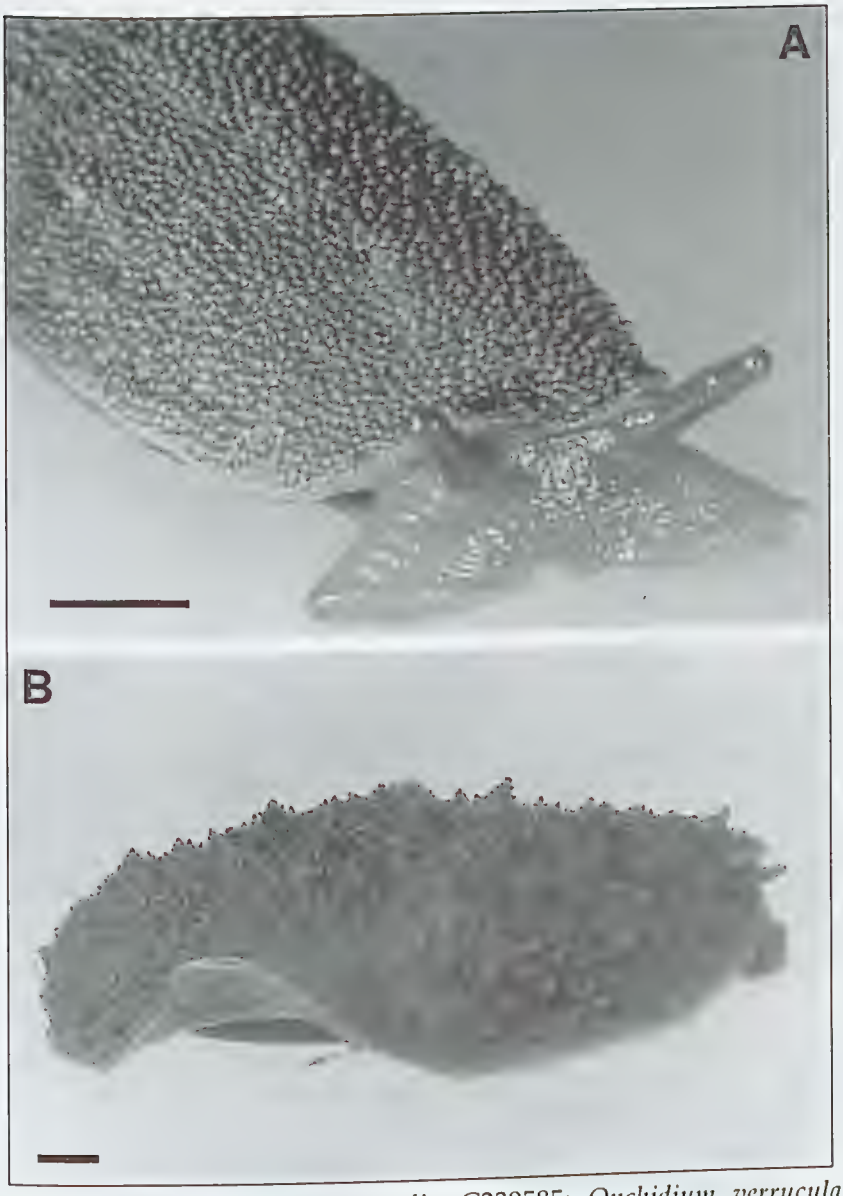
Two onchidiid species that are very similar externally can be found in a mangrove swamp in Careel Bay, Pittwater. They were identified by a study of internal and external characteristics. This paper records the differences found between the two species and identifies the external characters that can be used to identify these species.

Materials and Methods

Five specimens of each species were collected at Careel Bay, Pittwater. Voucher specimens were collected several months later and lodged in the Australian

Figure 1.
A. *Onchidina australis*, dorsal view. **B.** *Onchidina australis*, ventral view. **C.** *Onchidium verruculatum*, dorsal view. **D.** *Onchidium verruculatum*, ventral view. Scale 10 mm.

Figure 2. (see opposite page)
A. *Onchidina australis*. **B.** *Onchidium verruculatum*, with some of the eye-bearing papillae visible. Scale 5 mm.



Museum, Sydney (*Onchidina australis*, C339585; *Onchidium verruculatum*, C339586). Representaives of one of the species (*Onchidina australis*) were found above high tide mark, living in burrows under rocks, while the other (*Onchidium verruculatum*) was below high tide mark, again under rocks but in wet mud and without burrows. Each individual was killed by placing it in a solution of magnesium chloride and gradually increasing the concentration. They were dissected while fresh (*i.e.* prior to preservation) and the digestive and reproductive systems examined and drawn. Key works on the family Onchidiidae were then referred to and used to classify the two species. Diagrams from the works of Marcus (1971), Marcus and Burch (1965), Marcus and Marcus (1956), Stantschinsky (1907) and Plate (1893) were used to identify internal structures.

Results

A comparison of the external appearance of each species revealed small differences in colour and shape (Table 1, Figures 1-3), and also differences in the position of the pneumostome (Figure 4) and the presence or absence of accessory eyes (Table 1, Figures 1A, 1D, 3). The slight displacement of the pneumostome to the right (seen in the supralittoral species) is characteristic of *Onchidina* Semper 1882; in the other three New South Wales genera the pneumostome is in the mid-line (Bretnall, 1919). The presence of dorsal eyes is characteristic of *Onchidium* Buchanan 1800.

The supralittoral species exhibited a form of colour changing. When the specimens were first collected, they were not all the same colour. However, after some time in captivity, individual slugs became more and more similar. This was not seen in the intertidal species.

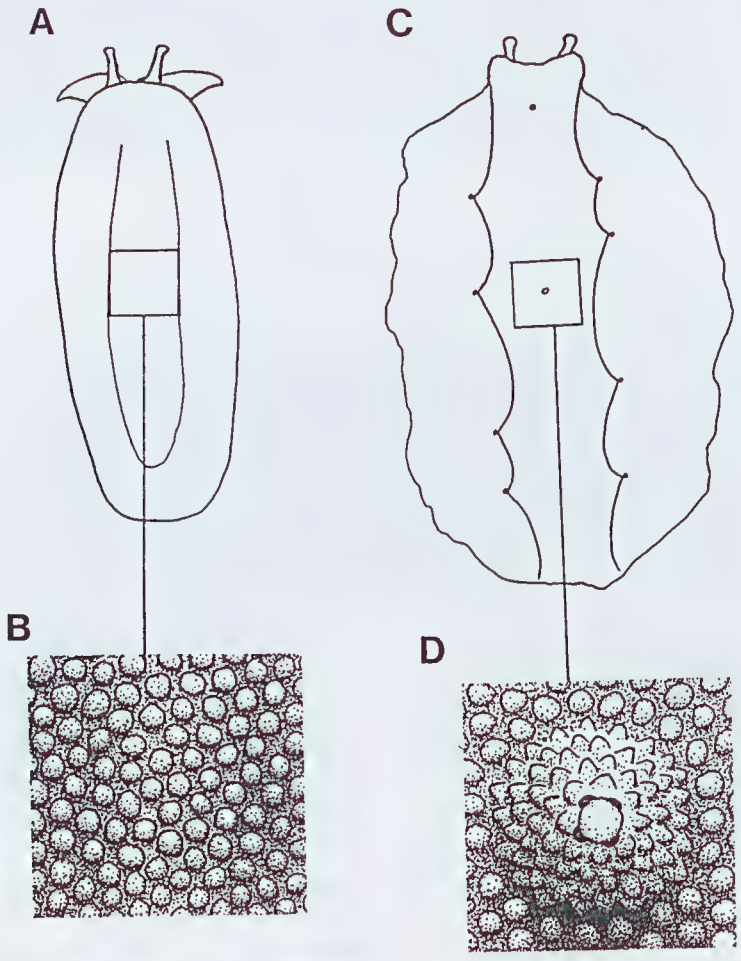


Figure 3.
Simplified dorsal view with a portion of the dorsum magnified to show the texture. **A.** *Onchidina australis*. **B.** Part of the dorsal durface of *Onchidina australis*. **C.** *Onchidium verruculatum*. Circles mark the positions of the accessory eyes. **D.** One of the dorsal papillae of *Onchidium verruculatum*, magnified to show the four accessory eyes.

Table 1
Comparison of the external features and the reproductive and alimentary systems of *Onchidina australis* and *Onchidium verruculatum*.

Characteristic	*Onchidina australis*	*Onchidium verruculatum*
External features		
Body shape	Body elongate, not very thick; firm and elastic to touch.	Body rounded, thick; soft to touch.
Dorsal surface	Contains small papillae that do not bear eyes; these are evenly spread and not restricted to the slightly raised section that runs down the middle of the dorsum (see Figures 1A, 3A).	Contains yellow-tipped papillae, each bearing three or four black eyes; these are found either at the edges of or within the raised portion of the dorsum (see Figures 1C, 3B). This middle area can be raised or lowered, particularly the eye-bearing papillae.
Dorsal colour	Olive-brown, with darker peripheral markings. The raised part is lighter and yellowish. There is some variation in colour; one specimen was much lighter.	Generally brown, but with variations including a uniform red-brown, or reddish markings.
Ventral colour	Head and foot yellow-brown; hyponotum highly reduced, dark grey-brown; mantle border with distinct yellow edge.	Foot and hyponotum blue-grey; mantle border gradually changing to yellow -brown.
Head	Head projecting freely from beneath the mantle; when fully protracted, both pairs of tentacles can be easily seen from above.	Head not projecting from the mantle border; eyestalks and sensory lappets barely visible, even when the slug is in motion.
Position of male reproductive opening	On the outside of the right eye-tentacle.	Towards the inside of the right eye-tentacle.
Pneumostome	Slightly to the right of the ventral midline (Figures 1B, 4A).	In the ventral midline (Figures 1D, 4B).
Internal features		
Salivary glands	Very large and filamentous.	Smaller, and leafy rather than filamentous.

Characteristic	*Onchidina australis*	*Onchidium verruculatum*
Stomach	Consisting of a very large crop (red in colour), a muscular gizzard and a digestive portion (Figure 7A).	Crop absent; gizzard and digestive portion present.
Intestine	Coiled in three loops (Figure 7A).	Coiled in two loops (Figure 7B).
Lungs	Occupying about one fifth of the body.	Occupying about one third of the body.
Reproductive system		
Ovotestis	Multiple, each kidney-shaped; vivid orange-brown.	Single, large, spherical; vivid orange-brown.
Hermaphrodite duct	One exits each ovotestis, then they merge. Each is highly coiled and white.	A single highly coiled duct; white.
Female system (Figure 5)		
Seminal receptacle	Small, granular, yellow.	Small, smooth, yellow.
Albumen glands	Paired; highly lobate but relatively small; yellow.	Paired; highly lobate and quite large; pink.
Spiral glands	Fine tubes, not tightly coiled; yellow.	Thick tubes, tightly coiled; white.
Spermatheca	Small and very firm, with a thick, coiled duct; white.	Large and very squalid, with a short duct; silvery-grey.
Male system (Figure 6)		
Vas deferens	About three times the length of the body; entering the body wall just above the spermatheca then emerging near the right eyestalk, before coiling first around itself and then around the penis.	About twice the length of the body; running through the body wall and entwining around itself and the penis.
Penis	Very long (almost the length of the body).	Short, about one fifteenth the length of the body.
Penial gland	Absent.	Very large. Attached to it is a highly coiled, very long tube, with an enlarged portion in the middle (Figure 6B).
Penis retractor muscle	Short.	Long.

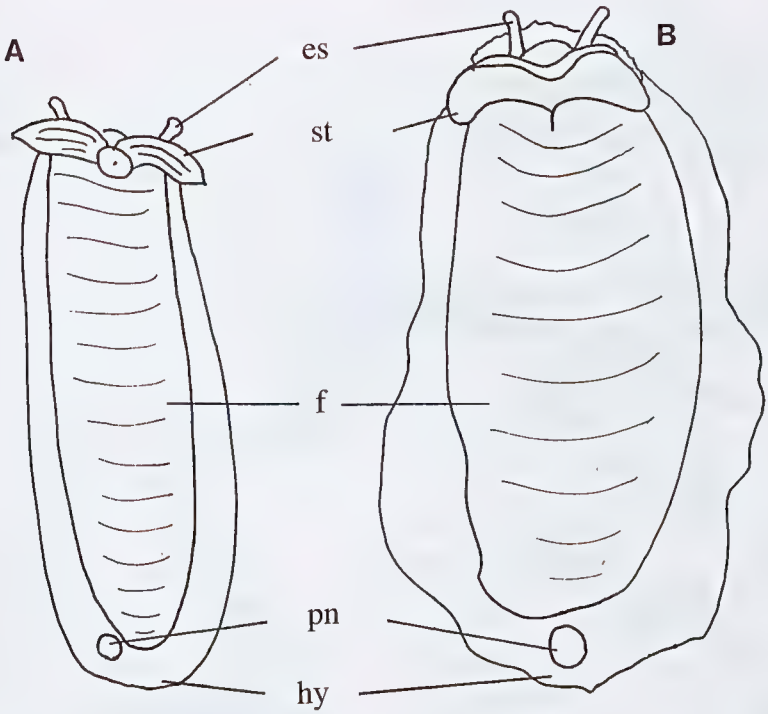


Figure 4.
Simplified ventral view showing the position of the pneumostome. **A.** *Onchidina australis*. **B.** *Onchidium verruculatum*. **es** - eyestalks, **f** - foot, **hy** - hyponotum, **pn** - pneumostome, **st** - sensory tentacles.

There were considerable differences between the reproductive systems of the two species (Table 1, Figure 5), especially the male structures (Table 1, Figure 6). The alimentary systems also contained some distinctive features (Table 1, Figure 7), especially in the coiling of the intestine.

Diagrams of the penis and vas deferens from Plate (1893) were used for final confirmation of the identification of the supralittoral species as *Onchidina australis* Semper 1882 and the intertidal species as *Onchidium verruculatum* Cuvier 1830. Both of these species were recorded from around Sydney by Dakin (1947).

Discussion

Onchidina australis and *Onchidium verruculatum* are similar in external appearance and can only be distinguished in the field by the position of the pneumostome and the presence or absence of accessory eyes. Both of these features have been previously noted (Bretnall, 1919). This study has also revealed slight but distinctive differences in the colour and shape of live specimens: *Onchidina australis* is elongate, and *Onchidium verruculatum* more rounded with a wider hyponotum. Previous notes on these features were often based on preserved specimens and are therefore not very reliable. However, Britton (1984) and Bretnall (1919) both state that *Onchidina* is very elongate with a reduced hyponotum while *Onchidium* is variable (oval to elongate oval).

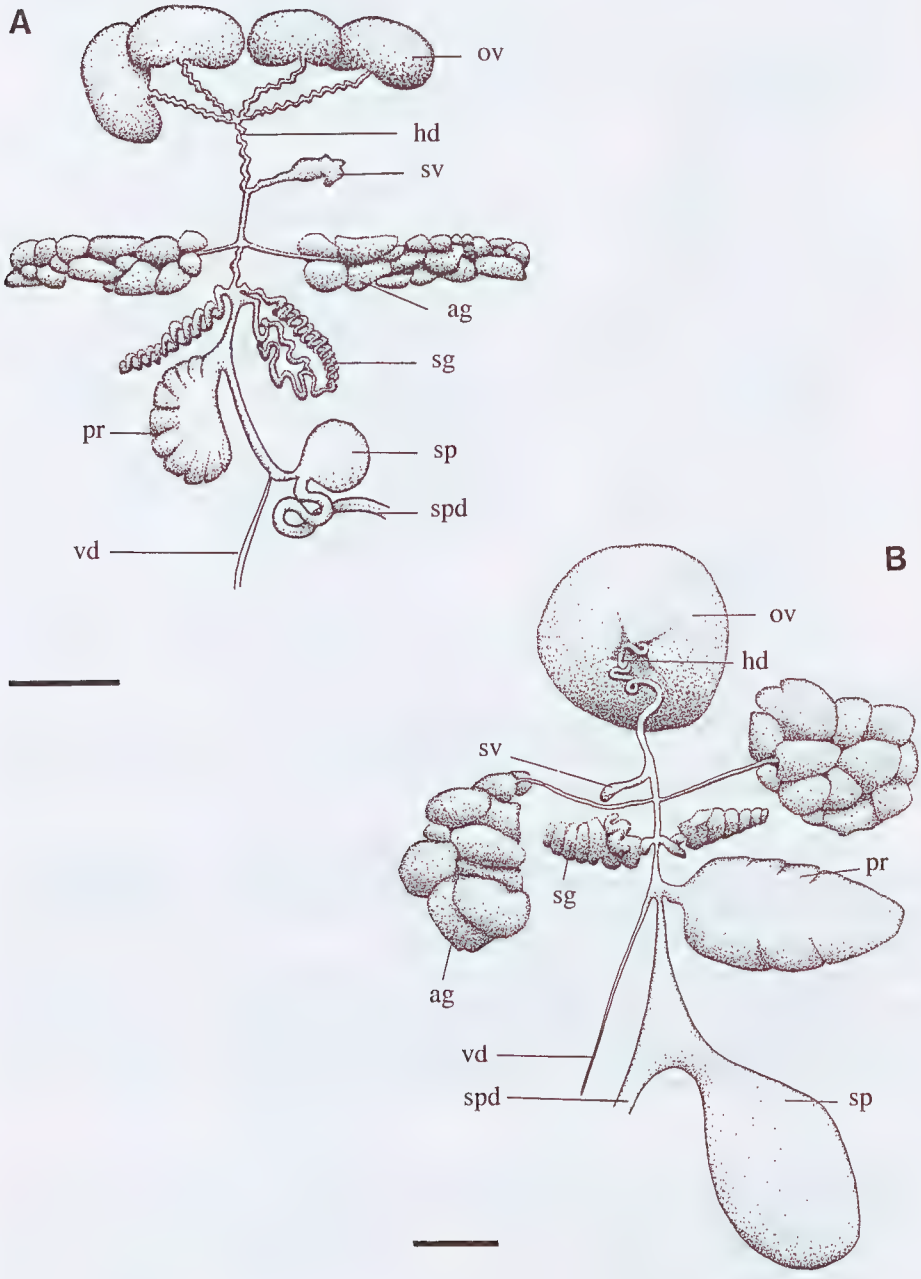


Figure 5.
Reproductive system. **A**. *Onchidina australis*. **B**. *Onchidium verruculatum*. **ag** - albumen gland, **hd** - hermaphrodite gland, **ov** - ovotestis, **pr** - prostate, **sg** - spiral gland, **sp** - spermatheca, **spd** - spermathecal duct, **sv** - seminal vesicle, **vd** - vas deferens. Scale 10 mm.

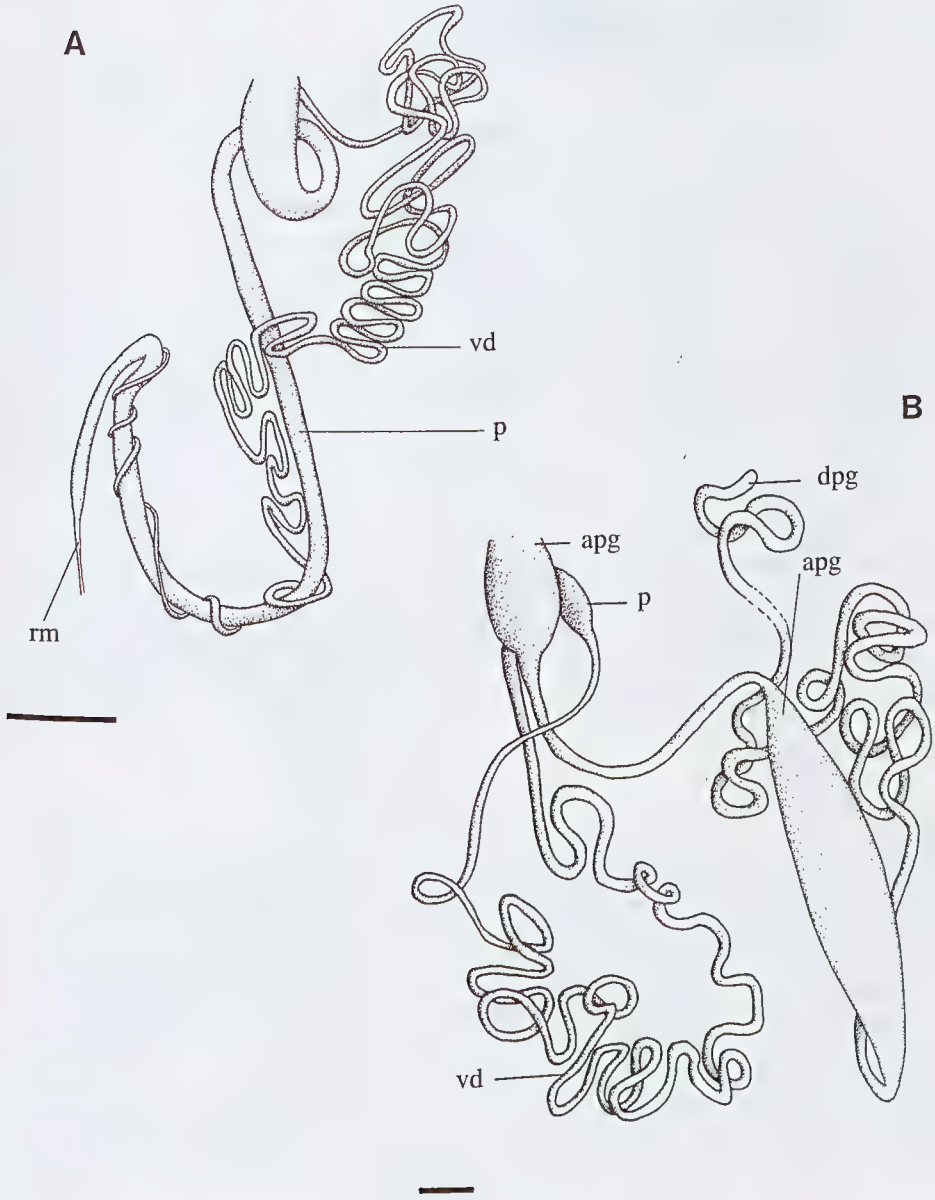


Figure 6.
Male portion of the reproductive system. **A.** *Onchidina australis*. **B.** *Onchidium verruculatum*. **apg** - accessory penial gland, **dpg** - duct of penial gland, **p** - penis, **rm** - retractor muscle, **vd** - vas deferens. Scale 5 mm.

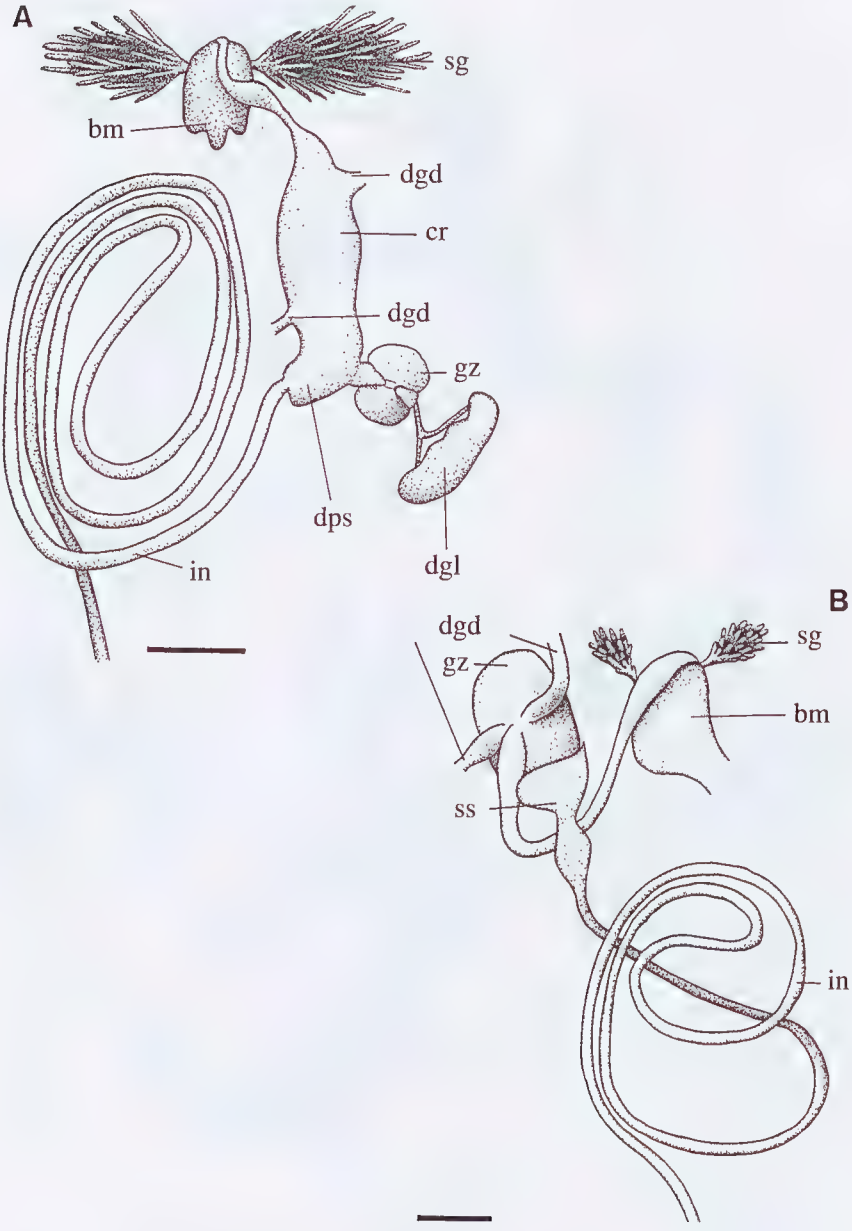


Figure 7.
Alimentary system **A**. *Onchidina australis*. **B**. *Onchidium verruculatum*. **bm** - buccal mass, **cr** - crop, **dgd** - digestive gland duct, **dgl** - lobe of digestive gland, **dps** - digestive portion of stomach, **gz** - gizzard, **in** - intestine, **sg** - salivary gland, **ss** - secondary stomach. Scale 10 mm.

The observed change in the body colour in *Onchidina australis* may be analogous to the colour changing properties of *Platevindex chameleon* and *Onchidium damelii*, which are mentioned by Bretnall (1919). This property has apparently not been observed in other species.

The male reproductive organs are commonly used to distinguish among members of the Onchidiidae, and were used by both Plate (1893) and Bretnall (1919) as the basis for their keys. Such features as the length of the penis and presence or absence of the accessory penial gland readily distinguish the two species in this study. There are also other useful characters, hitherto unmentioned, such as the number of lobes of the ovotestis (multiple lobes in *Onchidina australis*; only one in *Onchidium verruculatum*). The alimentary system also contains useful features. Labbé (1934) identified five gut types and proposed that these could be used to differentiate the different genera. It has since been argued that this is not the case, and different gut coilings are reported within one species (Britton, 1984). However, in general Labbé's type I is seen in *Onchidium* and type II in *Onchidina* (Britton, 1984), and this observation was supported by this study. In the two species examined here the gut type was found to be consistent within each species.

This study demonstrates that substantial differences exist between *Onchidina australis* and *Onchidium verruculatum*, even though they are similar externally. However, there are three other onchidiids found around Sydney, and in some areas more than two species can be found. In some parts of Southeast Asia up to twenty sympatric species can be found in mangroves (Britton, 1984), and many of these are poorly known. Considerable work remains to be done in identifying and describing these species, as no modern systematic treatments are available for this interesting group.

Conclusion

Onchidium verruculatum and *Onchidina australis* are not only very similar in external appearance but are also found in similar habitats. Important features such as the position of the pneumostome can be used to distinguish between the two species in the field, and there are also other internal characteristics such as aspects of the reproductive system that are diagnostic at the generic level. However, both species exhibited considerable variation in shape and colour, and given the substantial external similarity, they can easily be confused unless closely examined. Up to five species have been recorded in the Sydney area (Dakin, 1947), and it is apparent that a careful study of both internal and external characteristics from many more populations will be required to make a full assessment of the onchidiid fauna of even this small part of eastern Australia.

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Granicorium from Australian waters, with descriptions of a new species (Mollusca: Bivalvia: Veneridae)

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Abstract

Only two genera are represented in the venerid subfamily Samarangiinae, *Samarangia* and *Granicorium*, these are similar in appearance, being totally covered externally by an extraperiostracal layer (J.Taylor pers.com.) of agglutinated sand, they can be readily separated by the lack of lateral teeth in *Granicorium* (present in *Samarangia*). *Samarangia* contains the single species, *Samarangia quadrangularis* (A.Adams & Reeve,1850), which occurs throughout the Indo-Pacific. *Granicorium*, which is confined to Australian coastal waters has two species, *G. indutum* (Hedley, 1906), the type of the genus, and *G. citrinum* n.sp from northern Queensland. *G.attonitum* Iredale, 1936 is placed in the synonymy of *G.indutum*. The known range of *Granicorium indutum* is extended south from central Queensland to southern Western Australia.

Key words: Mollusca: Bivalvia: Veneridae, *Granicorium*, new species, Queensland

Introduction

Hedley (1906) described the genus *Granicorium* in an account of molluscs he had collected at Masthead Reef in the Capricorn Channel, southern Queensland, naming an unusual, sand covered species *Granicorium indutum*. In 1936, Iredale received deep water trawled specimens of *Granicorium* from off the Continental Shelf, north of Sydney, central New South Wales, which he named *Granicorium attonitum*. Examination of the syntypes of both species show the names to be synonymous, with *Granicorum indutum* the prior name. Mr Ian Loch, Collection Manager at the Australian Museum, has loaned *Granicorium indutum* material which extended the known range of the species from southern Queensland to southern Western Australia. This extension was confirmed by material in the Western Australian Museum. Additional *G. indutum* specimens have been obtained from shell dealers and trawlers which extend the range for the species to central Queensland. Examination of material recently trawled off Townsville, northern Queensland, revealed a previously unrecorded *Granicorium* species which differs from *Granicorium indutum*.

Material and Methods

All measurements were made using vernier dial calipers. Shell height given is from the umbones to the ventral margin on the left valve vertical to the hinge line. Shell length given is the greatest distance from anterior to posterior margin. Shell depth given is the greatest distance between the surfaces of the left and right valves. Shell size given is for the largest specimen examined by the author unless otherwise stated.

Abbreviations

AMS, Australian Museum, Sydney
KL, Lamprell Collection
QM, Queensland Museum, Brisbane
NSW, New South Wales
NT, Northern Territory
Qld, Queensland
lv, left valve
pv, paired or conjoined valves
rv, right valve
v, valves

Systematics

The systematic arrangement used for the family herein follows that of Lamprell & Whitehead (1992).

Family **VENERIDAE** Rafinesque,1815
Subfamily **SAMARANGIINAE** Keen,1968
Genus **Granicorium** Hedley,1906

Granicorium Hedley,1906: 477
Type Species: *Granicorium indutum* Hedley,1906.

Diagnosis: Similar to *Samarangia* in appearance, being totally covered externally by agglutinated sand but lacking lateral teeth.

Granicorium indutum Hedley, 1906.
(Fig.1a-d)

Granicorium indutum Hedley, 1906: 477, pl. 38, figs 26-27.
Granicorium attonitum Iredale, 1936; 278, pl. 20, fig. 17.

Description: Shell length to 50 mm; suborbicular, equivalve, solid, inflated; umbones prosogyrate; lunule broadly heart-shaped, moderately impressed; escutcheon wide, impressed; ligament internal, visible externally. Antero-dorsal margin very short, sloping, narrowly rounded at anterior margin; postero-dorsal margin widely convex, steeply sloping, narrowly rounded at posterior margin; ventral margin evenly and widely convex. Sculpture of numerous, strong, widely spaced, concentric growth ridges present in the extraperiostracal layer (J.Taylor pers.com.) of agglutinated sand. These ridges are fine and numerous under the extraperiostracal layer (J.Taylor pers.com.). Hinge plate broad. Hinge of lv lacking anterior lateral tooth; anterior cardinal tooth strongly curved anteriorly, thin and joined to median cardinal tooth at top, thickened at base, raised, peg-like, pit between anterior and median cardinal teeth wide, median cardinal tooth bifid at top, raised centrally, thicker at base; posterior cardinal tooth long, thin, curved, separated from median cardinal tooth at top; posterior lateral tooth thin, short. Muscle attachment scars well defined, anterior adductor scar pear-shaped, posterior adductor scar ovate. Pallial line entire.

Colour of shell under extraperiostracal layer (J.Taylor pers.com.) white; internally chalk-white medially, glossy marginally between muscle scars.

Material examined:
Type material: Lectotype (herein designated): 1 rv, 11 mm, AMS C 18868; figured by Hedley 1906; Masthead Reef, Capricorn Group, Great Barrier Reef, central Queensland, 31-37 m. Paralectotypes: 15 v, AMS C 203645, same data as lectotype.
New South Wales: AMS C 60638, 1 v, off Wattamolla, S of Sydney, 91-146 m (syntypes of *Granicorium attonitum*); AMS C 306370, 1 v, Shoalhaven Bight, NSW, 82 m. *Western Australia:* WAM S 1254, 15 lv, 11 rv, 48 km W.of Dongara, 29°11'S, 114°26'E, 49.9 m; WAM S 1255, 3 pv,1 lv, 7.5 mls W of City Beach, Perth, 37 m; WAM S 1256, 2 pv, 1 lv, SW of Coventry Rf, 18.2 m; WAM S 1257, 2 pv, Abrolhos Is. Zeewyk Channel, 38.2 m; WAM S 1258, 1 pv, Geographic Bay, 9.1 m; WAM S 1259, 1 rv, 10 mls W of Bernier Is. 73 m; AMS C 82812, 4 lv, 1 rv, E of Cheyne Bay, 34°55'S,119°0'E, 76 m. *South Australia:* AMS C 90541, 3 rv, 50 ml SW of Cape Adieu, Great Australian Bight, 32°42'S, 131°27'E, 144 m. *Queensland:* NTM (unregistered), 8 v, off Tugum Beach, 19-28 m; KL coll, 1 pv, off Cape Moreton, 131 m; KL Coll, 2 pv,1 rv, off Southport, 55 m; KL Coll. 1 pv, Capricorn Channel, 131 m; KL Coll, 3 pv, off Breaksea Spit, Fraser Isl. 60 m; AMS C 58369, 4 lv, 4 rv, North West Island, 23°18'S, 151°42'E, 36 m; AMS C 338107, 1.rv,1 lv, 3 kms NE of W. side Gillett Cay, Swains Reef, 21°42'S, 152°26'E, 73 m; AMS C 116519, 2 rv, 2 lv, 4 ml E of North Reef, 23°S, 151°58'E, 64 m.

Habitat: In sand to 72 metres.

Distribution: Off southern Western Australia, across the south, to central Queensland.

Measurements

	length (mm)	height (mm)	width of single valve (mm)
Lectotype *G.indutum*	11.0	10.0	3.0
Syntype *G.attonitum*	43.0	41.0	19.0
KL Coll.	25.3	23.0	8.0
	35.4	33.0	14.5
	45.0	42.0	16.0
	47.0	45.7	17.0
	49.2	46.0	19.0
	52.0	45.9	16.2
AMS C 58369	27.2	24.6	8.0
AMS C 82812	40.0	37.8	13.5
AMS C 9054	28.1	26.0	19.2
WAM S 1258	20.5	18.0	5.5
WAM A 1254	32.7	30.3	13.5
WAM S 1255	27.0	25.1	19.0

Remarks: Hedley described *Granicorium indutum* from small specimens obtained by trawling to 37 metres in sand off Masthead Reef, central Queensland. Comparison of *G. indutum* with *G. attonitum* obtained by Iredale from off Wattamolla, south of Sydney in 146 metres, showed that apart from the larger size and inflation of *Granicorium attonitum* the two species appear to be synonymous.

Granicorium citrinum n.sp
(Fig. 1e-h)

Etymology: For the colour of the external shell surface.

Description: Shell length to 27.3 mm; suborbicular, equivalve, solid; umbones prosogyrate; lunule broadly heart-shaped, strongly impressed; escutcheon wide, impressed; ligament internal, visible externally. Antero-dorsal margin very short, sloping, angulate at the anterior margin; postero-dorsal margin widely convex, steeply sloping, narrowly rounded at posterior margin; ventral margin evenly and widely convex. Sculpture of numerous, strong, widely spaced, concentric growth ridges present in the agglutinated sand extraperiostracal layer (J.Taylor pers.com.), fine and numerous under the extraperiostracal layer (J.Taylor pers.com.). Hinge plate broad. Hinge of lv without anterior lateral tooth; anterior cardinal strongly curved anteriorly, short, thin and joined to median cardinal at top, pit between anterior and median cardinal wide; median cardinal raised centrally, thick at the base; posterior cardinal long curved, separated from median cardinal at top; posterior lateral short. Muscle attachment scars well-defined, anterior adductor scar pear-shaped; posterior adductor scar ovate. Pallial line entire. Colour externally citreous; internally chalk-white medially, glossy marginally between muscle scars; extraperiostracal layer (J.Taylor pers.com.) grey.

Material examined:
Holotype: AMS C 203643, 1 pv, northern Queensland, 18°59.1S, 148°01.4E, 39 m, CSIRO Cruise "Lady Basten", stn 054, 5.9.97.
Paratypes: QM MO 62769, 2 pv, 19°11S, 148°02E, 59 m, CSIRO Cruise "Lady Basten", stn. 067, 6.9.97; AMS C 203644, 3 pv, 19°21S, 148°01E, 54 m, stn. 087, 8.9.97; KL coll 4 pv, 18°49S, 147°35E, 53 m, CSIRO Cruise "Lady Basten", stn 031, 3.9.97; WAM S 1366, 2 pv, 18°49S,147°35E, 53 m, CSIRO Cruise "Lady Basten", stn 031, 3.9.97.

Measurements

	length (mm)	height (mm)	width of single valve (mm)
Holotype *G.citrinum*	25.0	23.7	8.5
QM MO 62769	23.3	21.2	6.7
AMS C 203644	26.6	24.9	8.2
WAM S 1366	24.3	21.7	7.8
KL Coll	26.9	24.6	8.0

Figure 1.
1 (a-d). *Granicorium indutum* (Hedley) KL Coll; **a** - external rv, length 25.0 mm; **b** - internal rv (showing teeth); **c** - internal lv (showing teeth); **d** - anterior margin of shell showing lunule and inflation. **1 (e-h).** *Granicorium citrinum* KL Coll; **e** - external rv, length 25.0 mm; AMS C 203643, holotype, **f** - anterior margin of shell showing lunule and inflation, length 26.6 mm; **g-h** - AMS C 203644; **g** - internal rv (showing teeth), **h** - internal lv (showing teeth) length 26.9 mm.

Habitat: In sand to 59 metres.

Distribution: northern Queensland.

Comparative remarks

Numerous specimens of *Granicorium citrinum* were compared with small specimens of *G. indutum* of approximately equal size. *G.citrinum* could be separated from *G. indutum* by its consistently smaller adult size and less inflated shell, the posterior margin relatively longer and straighter and the umbones less prominent. In *G.citrinum* the lunule is better defined and more sunken than in *G.indutum*, and the posterior lateral tooth is shorter and thinner than in *G. indutum*. The external colour of *G.citrinum* is consistently yellow under the sand coloured extraperiostracal layer (J.Taylor pers.com.), while in *G. indutum* the external colour is white.

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Histological investigations on *Dendrodoris nigra* (Stimpson, 1855) (Gastropoda, Nudibranchia, Dendrodorididae)

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Abstract

The histology of the major organ systems (digestive, reproductive, nervous, circulatory, excretory and respiratory, as well as epidermis) of the nudibranch *Dendrodoris nigra* (Stimpson, 1855) are described for the first time and the results are compared with those derived from other members of the Doridoidea. It is shown that some characters which have been used to differentiate the genus *Dendrodoris* Ehrenberg, 1831 from other doridoideans (i.e., retractability of gills, lack of hard structures in the anterior digestive system, presence of pericardial glands) are problematic when used for phylogenetic analysis. This is especially true when taking into consideration that little is known about details of these structures in the Doridoidea as a whole.

Key words: Nudibranchia, Doridoidea, *Dendrodoris nigra*, histology, phylogeny

Introduction

Two recent papers dealing with the taxonomy of species belonging to the genus *Dendrodoris* Ehrenberg, 1831 have clarified the taxonomy of species from the Indo-Pacific (Brodie et al. 1997) and the Atlantic (Valdés *et al.* 1996), and demonstrated complexes of highly variable species in both instances. Although the external features may be very variable in some species e.g. *Dendrodoris nigra* (Stimpson, 1855) and *Dendrodoris grandiflora* (Rapp, 1827), the internal organ systems seem to be rather more conservative with relatively little variation (Brodie *et al.* 1997). Furthermore, a comparison of the organ systems of different *Dendrodoris* species shows that *Dendrodoris* is a well marked genus within the family Dendrodorididae O'Donoghue, 1924. The synonymy and validity of genera within the Dendrodorididae have been reviewed recently (Valdés *et al.* 1996; Valdés & Ortea 1997).

The family Dendrodorididae is unusual within the Doridoidea in that it lacks cuticular structures within the buccal mass. This character is shared by the Phyllidiidae Rafinesque, 1815, a family with secondary gills on the ventral side between the notum and the foot. The absence of jaws and radula is the single character which, according to Bergh (1876), unites these two families, and for which he created the taxon Porostomata. Although many authors have followed his classification (Pruvot-Fol 1954, Odhner in Franc 1968, Schmekel & Portmann 1982, Thollesson 1998), some mentioned doubts and considered the taxon an artificial grouping (Brunckhorst 1993, Rudman 1998). Since only the lack of characters unites these two rather different families, there is a demand for further characters to support or to falsify the relationship. Brunckhorst (1993: 84)

came to the conclusion, after analysing the phylogenetic relationship within the Phyllidiidae, using *Dendrodoris* and *Chromodoris* as outgroups, that *Dendrodoris* shared more derived characters with the Cryptobranchia than with the Phyllidiidae. He concluded "the grouping of dendrodorids and phyllidiids together as the Porostomata is untenable.... The Dendrodoridídae clearly belong with other doridoids ... but their phylogenetic position is yet to be clarified." This view was diametrically opposed by Valdés (1996) who stated that "the superfamily Porodoridoidea is a monophyletic group" and that "the loss of the radula has only occurred once in the evolution of the dorids. " There is no doubt that this situation requires further clarification.

In this paper we present characters of *Dendrodoris nigra* which are difficult to find by macroscopic investigation and which will help to elucidate the phylogenetic relationship of the Dendrodoridídae. Although we present several characters in a new light, it is evident that only after investigating many more members of the Doridoidea with the same thoroughness that the relationship of the Dendrodoridídae can be determined.

Material and Methods

Three specimens of *Dendrodoris nigra* (length of living specimens 23, 43, 53 mm) from Dingo Beach ,(Queensland, Australia, collected by the authors in August 1995 and July 1997) were embedded in hydroxyethlymethacrylate for serial sectioning (2-3 (m). Sections were stained with toluidine blue. Comparisons were made with sections of other doridoideans belonging to the Cryptobranchia and Phanerobranchia. For anatomical drawings and general description of the organ systems of *D. nigra* the reader is referred to Brodie *et al.* (1997).

Results

Epithelia

Epidermis: The dorsal notal epithelium consists mainly of high columnar to flask-shaped cells with basally lying nuclei (Fig.1A). The cytoplasm stains homogeneously light blue to transparent without further differentiation. Cells of similar size with several smaller, light blue staining grana and cells with a dark violet staining network (cells producing acid mucopolysaccharids) are interspersed. Very few ciliated cells can be observed. Black pigment grana, which obviously are not confined to a certain cell type, are located in the connective tissue of the notum beneath the basal lamina of the epidermis. The epithelium on the ventral side of the notum shows similar cell types, but the cells are less tall. In the dorsal area, the epithelium very often forms grooves or invaginations, which do not differ in their cellular appearance from the rest of the epithelium (Fig. 1B). Subepithelial glandular follicles composed of one or several cells are present in the lateral part of the notum. These glandular cells are similar in appearance to the acid mucoploysaccharide producing cells in the epidermis, but staining slightly darker.

Rhinophores: The epithelium consists of small, prismatic cells with basally lying nucleus and no visible differentiation of cytoplasm. Some glandular cells are interspersed, containing a large light blue staining vacuole. The margins of the

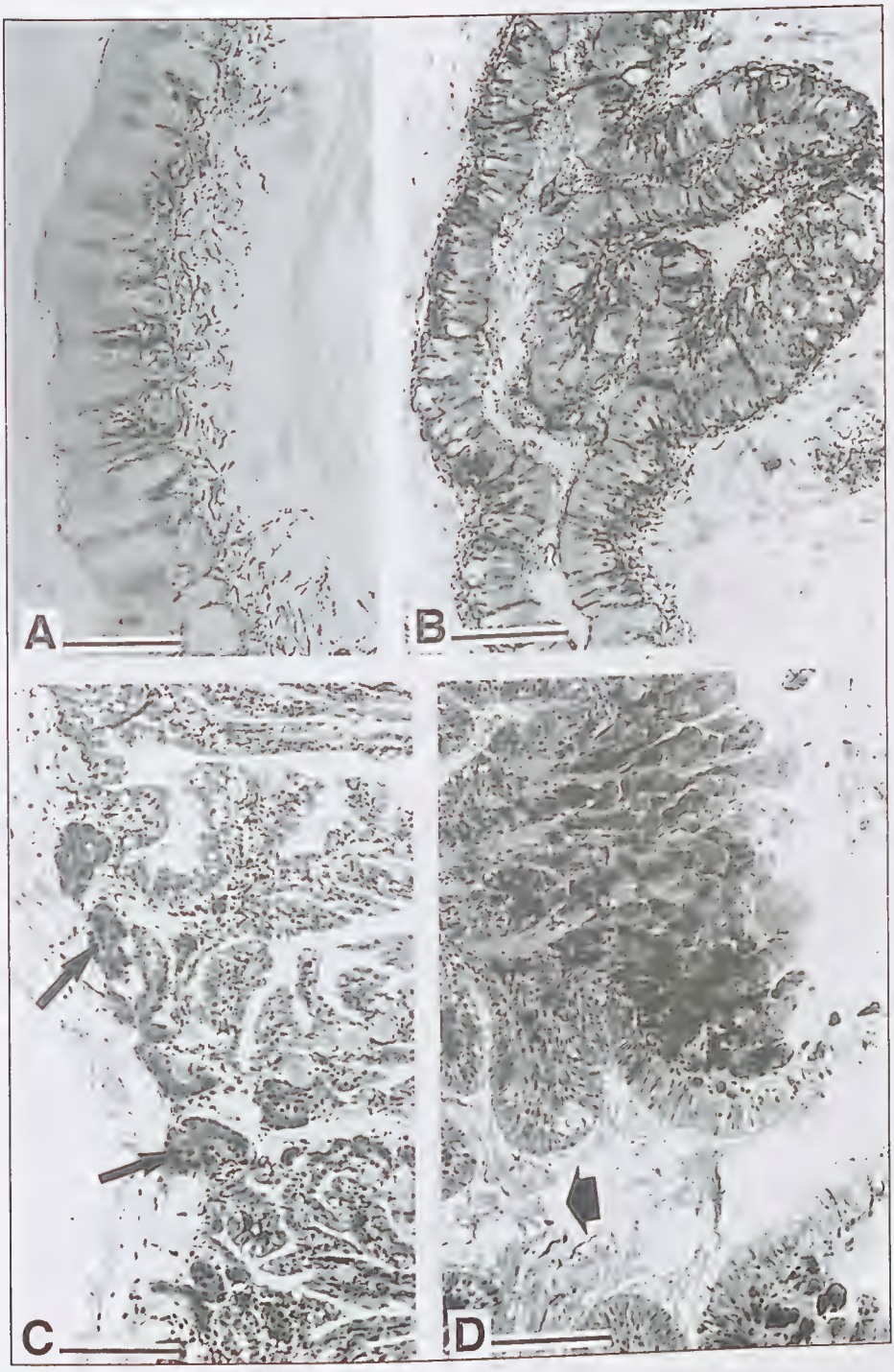

Figure 1.
Dendrodoris nigra. Epithelia. **A**, dorsal notum epithelium with underlying black pigment granules; **B**, dorsal notum epithelium of an invagination; **C**, basal part of gills with gill glands (arrows); **D**, glandular follicles around the mouth; arrow indicates the direction to the mouth. Scale bars: A 50 μm, B-D 100 μm.

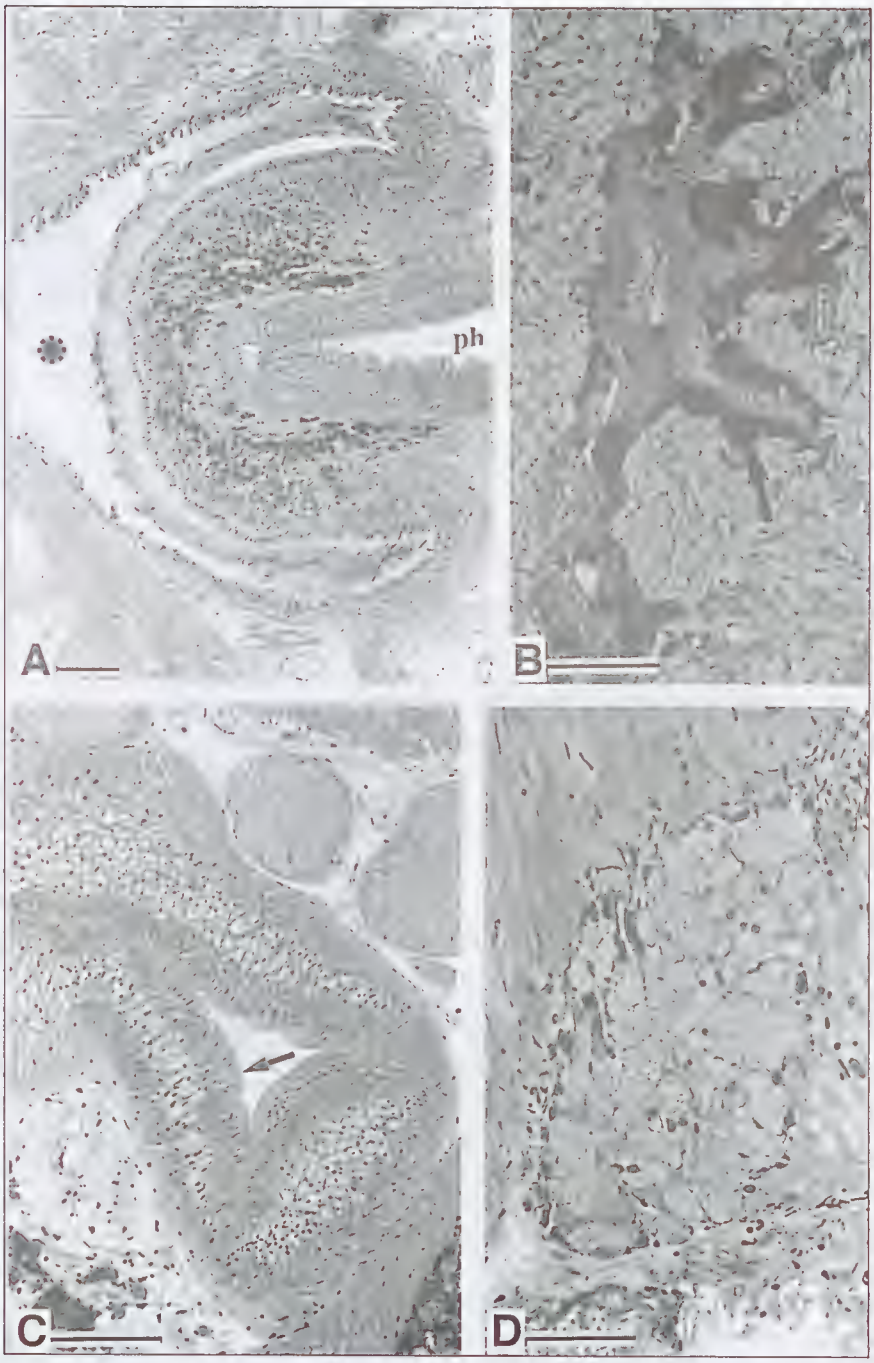

Figure 2.
Dendrodoris nigra. Digestive tract. **A**, transverse section of labial disc with pharynx on the right and oral tube (asterisk) on the left side; **B**, oral gland with cross section of collecting ducts, annexed glandular area staining dark (arrow) and glandular area staining light; **C**, semi cross section of pharynx; cuticular lining (arrow) barely visible; **D**, cross section of right salivary gland. Abbreviations: **ph** - pharynx; Scale bars: A-C 100 μm, D 50 μm.

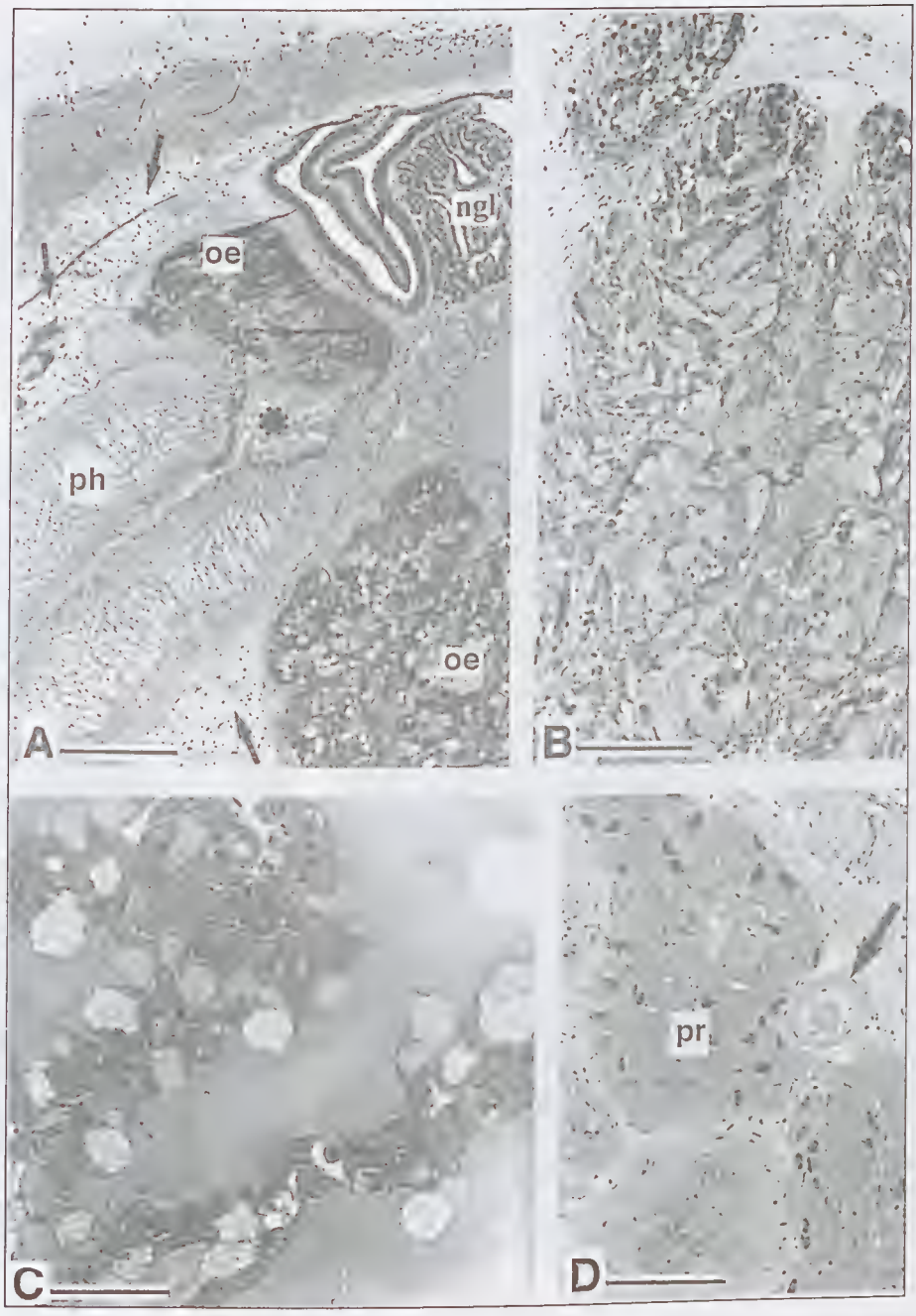

Figure 3.
Dendrodoris nigra. **A**, cross section showing transition from pharynx into oesophagus (asterisk) with proximal part of oesophagus above the asterisk and on bottom on right side, juvenile nidamental glands and oral gland on the left side above pharynx (arrows); **B**, part of distal oesophagus; **C**, cross section of digestive glandular lobes, **D**, cross section of vas deferens (arrow) and prostatic duct with subepithelial lying glandular follicles of prostate gland. Abbreviations: **ngl** - nidamental glands, **oe** - oesophagus, **ph** - pharynx, **pr** - prostate gland; Scale bars: A-D 100 μm.

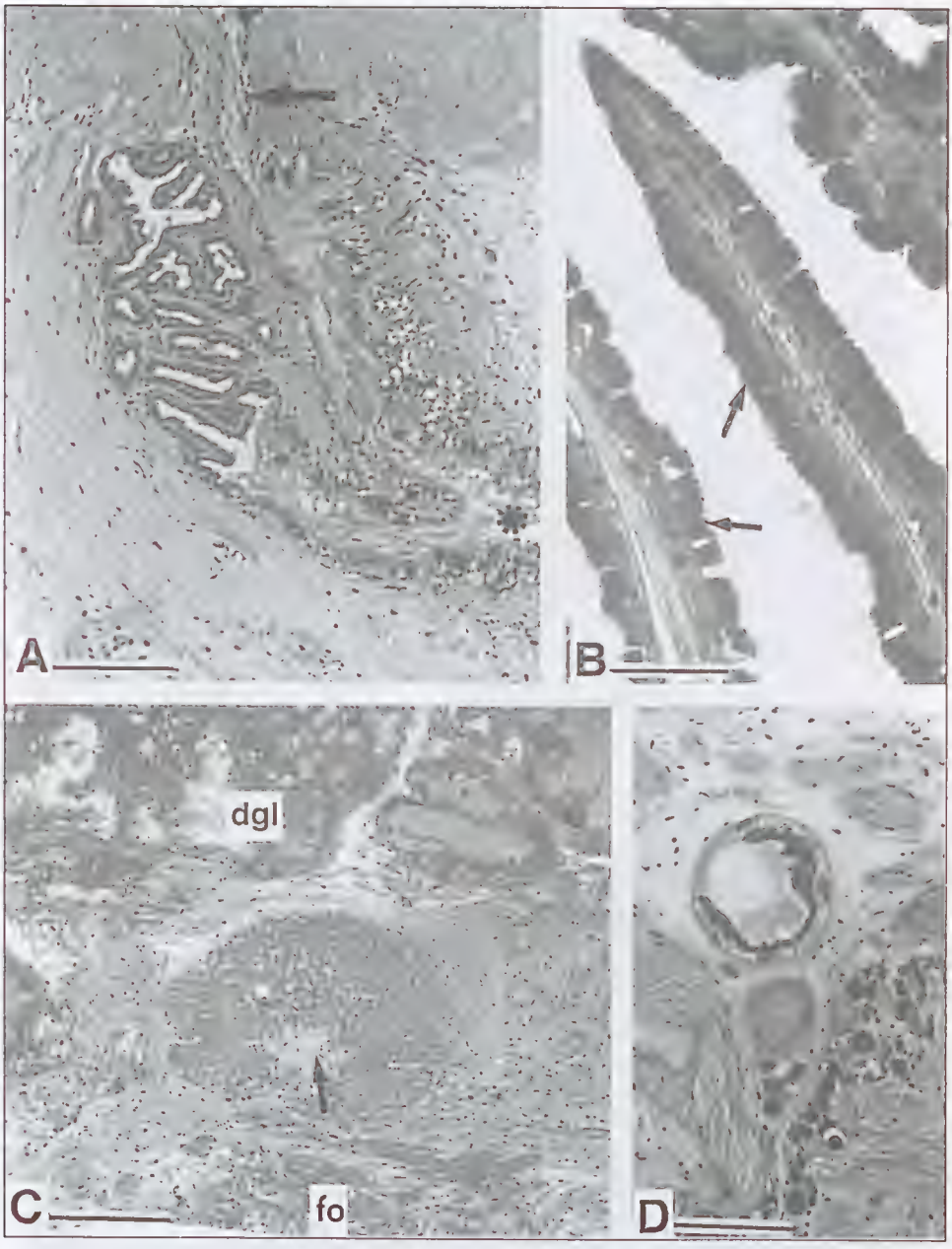

Figure 4.
Dendrodoris nigra. **A**, vestibular gland of immature specimen; asterisk indicates the opening into the vestibulum; arrow indicates the distal oviduct; **B**, detail of vestibular gland of mature specimen; epithelium showing a high microvilli border (arrows); **C**, blood vessel situated between the fused retractor muscles (arrow).; **D**, eye with optic ganglion beneath and cerebro-pleural complex on right side. Abbreviations: **fo** - foot, **dgl** - digestive gland intermingled with excretory system. Scale bars: A, C-D 100 μm, B 50 μm.

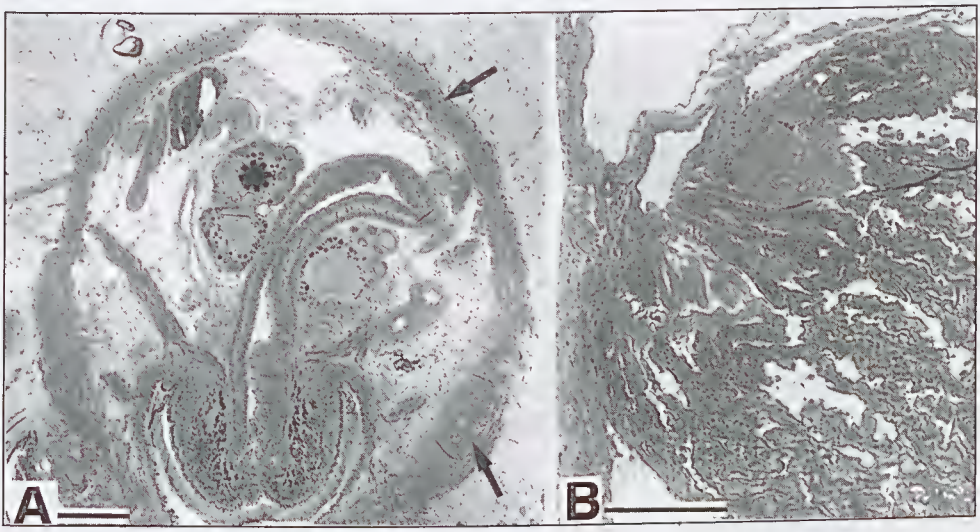

Figure 5.
Dendrodoris nigra. **A**, cross section of anterior part of body, showing body cavity framed by a thick muscle layer (arrows), labial disc with pharynx, pedal ganglia on both sides of the pharynx and the pleural (asterisk) only on the left side; **B**, cross section of syrinx. Scale bars: A-B 100 μm.

rhinophoral lamellae of one animal shows few larger cells containing non-staining vacuoles, similar to the special vacuole cells of other Doridoidea (see Wägele 1998).

Foot epithelium: The cells are tall and ciliated, with nuclei lying basally to medially. Few epithelial glandular cells with violet staining grana are present. Subepithelial glandular follicles with two to four glandular cells containing blue to violet grana are very common.

Gill (Fig. 1C): The epithelium consists of cuboidal cells with large nuclei. Glandular cells, which stain homogeneously light blue or have violet grana, are interspersed. Ciliated cells are also present. Gill glands (Fig. 1C, arrows) are present at the bases of the gills. They are composed of many cells with bluish contents and large nuclei. The gills are underlaid by thick muscle layers, concentrating anteromedian first in one U-shaped muscle, later separating into two strings running ventrally to the head region.

Digestive tract

Oral tube: The epithelium consists of high columnar cells interspersed with some glandular cells with bluish contents and a few glandular cells containing violet grana. A thick glandular layer, composed of pyriform glandular follicles filled with grana of rather uniform size, staining bluish violet, surrounds the mouth area (Fig. 1D).

Labial disc (Fig. 2A): The labial disc is not covered by a cuticle. Scattered glandular cells containing vacuoles uniformly staining violet can be observed. Two strong muscles insert at the labial disc (Fig. 5A).

Oral (ptyaline) gland (Fig. 2B): the oral gland is formed by a thick layer of glandular cells resulting in a spongy appearance. The large vacuoles in these cells, which have pycnotic nuclei, do not stain. Along the outgoing ducts glandular cells with bluish contents can be observed. The two main ducts are characterized by a thick ring muscle layers. After fusion of these ducts, the common duct leads ventrally along the pharynx within the labial disc and opens into the lumen of the oral tube.

Pharynx (Fig. 2C, 3A, 5A): The pharynx is tube-like and long and is composed of several layers. From outer to inner side following layers can be observed: exterior circular muscle layer with areas of transverse muscles; layer of cells with large vacuoles giving the appearance of a network; layer of circular muscles; pharyngeal epithelium without any glandular cells; thin cuticle.

Salivary glands (Fig. 2D): The salivary glands form a rather compact circle around the transition between pharynx and oesophagus. Only one microscopic duct leading into the pharynx is observable. No distinct lumen within the glandular tissues is visible, and no distinct arrangement of glandular cells into an epithelium is discernible. The glandular cells exhibit a medium sized functional nucleus, less commonly a pycnotic nucleus. They are completely filled with densely packed, very light blue staining grana, showing a superficial similarity to the oral glandular tissue.

Oesophagus (Fig. 3A, B): The oesophagus is surrounded by a layer of circular and longitudinal muscle fibres of varying thickness. No lumen is observable throughout the oesophagus except for the most anterior part, which is filled with pink secretions. It is difficult to describe the number of different glandular cell types, since all different types may represent different functional phases of one and the same type. Following phases are discernible: cells with blue to violet staining large vacuoles; cells with reddish to violet staining large vacuoles; cells with different coloured (from pink to light violet) but rather homogeneously staining cytoplasm.The nuclei always lie basally.

A further glandular cell type with filiform contents, staining dark violet, is present in the anterior part of the oesophagus (Fig. 3A). In the distal part of the oesophagus, the cells with homogeneously staining contents dominate (Fig. 3B). The whole oesophagus is underlaid by an extremely thick muscular layer.

Stomach: Especially at the entrances into the digestive gland, the stomach wall is folded. The epithelium is composed of small, elongate and ciliated cells with small, elongate, basally lying nuclei.

Digestive gland: Many entrances from the stomach area into the digestive gland are visible. Probably only one type of glandular cells is present in the digestive gland, since transitional stages can be observed: early stage cells contain small bluish grana or vacuoles, increasing in size in the following phases and forming a grape-shaped (clustered) structure, now staining more greenish to light blue (Fig. 3C). When contents of vacuoles is emptied, small spaces or areas with microscopic grana staining violet remain.

Caecum: No caecum (transformed right digestive gland) opening into the stomach is distinguishable.

Intestine: The inner wall of the intestine is folded throughout its length. After its origin from the stomach the intestine is especially highly convoluted. No typhlosole is discernible. The epithelium consists of elongate, non-glandular cells, with long cilia and basally to medially lying nuclei. Some violet staining glandular cells are interspersed in the proximal part of the intestine that follows after bending and running posteriorly. The intestine is surrounded by a layer of circular muscles followed (inwards) by a ring of longitudinal muscles. No specialization of cells is discernible in the area where the intestine bends and then runs posteriorly, called caecum or pyloric gland by different authors respectively (Brodie *et al.* 1997; Valdäs *et al.* 1996).

Reproductive system

Gonad and ampulla: The gonad forms an incomplete layer over the digestive gland, with parts extending deep into the digestive glandular tissue. In cross section the digestive glandular tissue appears intermingled with gonad and kidney. The ampulla is sausage-shaped and filled with autosperm. The epithelium of the ampulla is composed of cuboidal to flat cells.

Distal genital tract: The vas deferens shows a thick tubular prostate gland. The glandular cells lining the duct are elongate, filled with light blue staining grana and basal nuclei. A dense ciliation is present within duct. Subepithelial glandular cells are enormous, of similar appearance as the epithelial glandular cells, but with large nuclei, arranged into follicles (Fig. 3D). The proximal and distal sections of the vas deferens (non-prostatic parts) are lined by an epithelium with cuboidal, ciliated cells only. A layer of circular muscles surrounds the non-glandular parts. No cuticularized penial structures (i.e. cuticular lining and/or spines) are visible in any of the specimens investigated.

In the smaller specimen the female mass is not differentiated into distinct glands (Fig. 3A), but in the two larger ones it is composed of three distinct parts, namely the capsule gland, proximal and distal mucous glands. The capsule gland consists of numerous narrow coils. The cells of the epithelium are broad and columnar containing numerous, large, light-blue staining granules.

Spherical to elliptic nuclei are lying at the base of the glandular cells. Supporting cells with short cilia are alternating with the glandular cells. The proximal mucous gland is connected to the capsule gland by a long coiled duct lined by densely ciliated cells. The epithelium of the proximal mucous gland is folded in narrow coils similar as in the capsule gland. The glandular cells are prismatic and contain heterogeneous mucous secretions staining purple or dark red. Supporting cells bear very long cilia. The distal mucous gland is composed of various parts with different staining properties. These may represent various functional stages and are therefore difficult to interpret. All glandular cells of the distal mucous gland contain purple to red staining mucous secretions. The basally lying nuclei of the glandular cells are pycnotic. The supporting cells have long cilia.

The opening of the oviduct lies more caudally than the openings of the vagina and the vas deferens. The vaginal duct is narrow and opens proximally into the vestibulum next to the vas deferens. The epithelium of the bursa copulatrix is composed of apocrin secreting cells. Only a few muscle cells surround the bursa. The receptaculum seminis is filled with allosperm, these being orientated but not attached to the folded wall. Contrary to the bursa, a distinct layer of muscles surrounds the receptaculum.

In the smaller specimen, the vestibular gland lies completely within the notal tissue and therefore is not visible anatomically in this animal (Fig. 4A). In the larger specimens, it intrudes into the visceral cavity as a compact mass. The cells are small, elongate, with basally (in smaller) to medially lying nuclei (in larger specimens) and apically lying, microscopic, violet-staining grana. The cells in the larger specimen exhibit a brush-like appearance (Fig. 4B).

Nervous system

The circumoesophageal central nervous system, with fused cerebral and pleural ganglia, surrounds the pharynx (Fig. 5A). All ganglia are surrounded by a thin layer of connective tissue. Nerve cells are concentrated in the periphery of the ganglia. The statocyst has many elongate otoconia (length about 5 μm). The eye is connected to a small optic ganglion by a very short optic nerve (Fig. 4D).

Circulatory system

In the anterior dorsal wall of the pericardium folds ("pericardial glands") are present, which are not glandular, but are composed of tiny cells and small nuclei being similar in appearance to those of the connective tissue.

A single, well formed blood vessel is present, which runs anteriorly in the ventral side of the muscle layer surrounding the visceral cavity, and posteriorly within the two fused gill retractors (Fig. 4C); sending ducts into the foot in two directions.

The blood gland is characterized by minute cells and nuclei, forming a rather compact mass on the right side of body next to the cerebropleural complex, with lacunae interspersed.

Excretory system
The bulb-like syrinx is extremely large, being approximately equal in size to the gill chamber in cross section. Only in the apical part longitudinal folds with cilia are present, whereas the basal section exhibits folded lamellae (Fig. 5B). The tissue of the kidney is not only surrounding the whole digestive gland, but also intruding into it and intermingled with the gonad in many areas.

Black pigment
The black pigment is not confined to a certain cell type. Pigment granules are widely distributed within the connective tissue and around the viscera, beneath external epithelia (including rhinophores and gills), in the peritoneal wall, between subepithelial glandular follicles around the mouth opening, within the blood gland and in the thick muscle layer surrounding the visceral cavity.

Rhogocytes
Cells with a spindle-shaped appearance filled with dark stained granules of different size and a medium sized nucleus are present throughout the notal tissue.

Discussion
Dendrodoris nigra differs not only in its anatomy from other Doridoidea (Valdés *et al.* 1996, Brodie *et al.* 1997) but also in its histology. Contrary to many other doridoideans, the epithelium of the notum consists mainly of a glandular cell type which, according to its bluish staining, does not produce acid mucopolysaccharides. Glandular cells that do produce acid mucopolysaccharides (violet staining) are interspersed with those non-glandular cells. Avila and Durfort (1996) investigated the lateral notal epithelium of *D. limbata* by electron microscopy. They also described two different types of secreting cells. The type they called mucous cell is probably the same one that is identified as secreting acid mucopolysaccharides here. They called the second type "macrovacuolated cells" and assumed that these cells are responsible for the synthesis, storage and secretion of defensive substances. We assume that this is the dominant cell type described here and which is filled by light blue contents. We can confirm the results of Avila and Durfort (1996) on the concentration of subepithelially lying glands in the lateral part of the notum producing acid mucopolysaccharids; these are less conspicuous in the smaller animal.
No special vacuolated cells (vacuolated cells Wägele 1998 = "Spezial-vakuolen-zellen" Schmekel 1982) were present in either the mantle or the rhinophoral epithelium where they can usually be found. Presence of special vacuolated cells is a character that unites all members of the Nudibranchia (Schmekel 1982, Wägele 1997 & 1998). Avila and Durfort (1996) did not mention any special vacuolated cells in their descriptions on the epithelia of the notum and rhinophores of *Dendrodoris limbata*. The presence of somewhat higher vacuolated cells on the margins of the rhinophoral lamellae in one of our specimens indicate that special vacuolated cells may be present, but this has to be confirmed by ultrastructural investigations. If these cells really are those described by

Schmekel (1982) and Wägele (1998), then they differ in their size from the typical special vacuolated epithelium.

Gill glands are present in many Cryptobranchia (*Jorunna, Hypselodoris*) and Phanerobranchia (*Corambe, Onchidoris, Roboastra*). The absence is confirmed only for *Limacia clavigera* (Wägele 1998) amongst those nudibranchs investigated to date. Wägele (1997) considered the presence of gill glands as a synapomorphy of the Doridoidea. The genus *Dendrodoris* shares this character with all other doridoideans and is therefore indisputedly part of this clade.

Dendrodoris species can retract their gills completely. At least in *D. nigra* investigated here, the muscles responsible for this retraction are grouped first into several, then into just one, U-shaped retractor which runs along the ventral side before it separates again into two parallel stripes running ventrally in the area of the head. Up to now, this is the only species where muscles of this type and magnitude have been described (unpublished results of senior author). *Bathydoris* has no muscles in the gills or the gill base, whereas some Phanerobranchia do have muscles within the gills or gill base (*Limacia, Roboastra*). In *Onchidoris*, a member of the Phanerobranchia with nearly contractile gills, two larger retractors exist. The cryptobranchs *Jorunna, Hypselodoris* and *Discodoris* also have two main retractors, which run anteriorly on the ventrolateral sides within the musculature surrounding the visceral cavity. Although the retraction of gills into a cavity is considered to be an autapomorphy of the Cryptobranchia, we find similar features in phanerobranchs, as well as in *Dendrodoris*. The presence of just one retractor muscle in the posterior part, which runs immediately to the ventral side in *D. nigra* is a quite different situation compared to the two lateral muscles in other Cryptobranchia. Two different evolutionary trends can be discussed. First it can be assumed that the two retractors in *D. nigra* represent the two separated retractors of members of the Cryptobranchia, but in the former they migrated to the ventral side and fused at least partly. Secondarily one can interpret them as homologous structures that evolved in parallel. Then they evolved from primarily homologous muscles present in nearly all Doridoidea to form retractors that do not have the same position as the retractors of the Cryptobranchia or Onchidoridiidae, but having the same function.

Paired oral glands are present in several groups of Nudibranchia, but only a few have a common duct opening on the ventral side into the oral tube, e.g. *Armina* (Kolb 1998), *Hancockia* (Hoffmann 1939), *Calma, Spurilla, Berghia, Facelina* (Dreyer 1913). According to observations on the histology of oral glands in general (unpublished results of senior author), the spongy appearance of the glandular tissue in *Dendrodoris* seems to be unique and therefore a homology with other oral glands cannot be taken for granted. The evolution of a paired oral gland with one efferent duct in the Dendrodorididae is considered to have occurred independently from other nudibranchs with oral glands.

The very large labial disc that is not covered by a labial cuticle marks the transition from the oral tube into the pharynx. Evidence for homology of the elongate, tubular pharynx in *Dendrodoris* and the (usually) short, bulbous

pharynx of other dorids is given both by the net-like tissue of the whole pharynx in *Dendrodoris*, which is very similar to the radula bearing cushions of other members of the Doridoidea, and by the cuticular lining.

Valdés *et al.* (1996) misinterpreted the different parts of the proximal digestive system. They used the term pharyngeal bulb for a part which represents the oral tube and they described the pharynx (anterior to the salivary glands) as part of the oesophagus. Our histological results definitely show the homology of the anterior parts with the muscular bulb of other radular-bearing gastropods.

Usually the salivary glands have a uniform structure in Nudibranchia, with at least two different types of glandular cells, one of them producing acid mucopolysaccharides (unpublished results of senior author). *Dendrodoris nigra* has only one type which, according to the staining results, does not produce acid mucopolysaccharides. So, the structure of the salivary glands, as well as their histology, seems to be unique within the Nudibranchia.

The oesophagus of *Dendrodoris nigra* (and also *D. fumata*, unpublished results) is also unique in its structure, having virtually no lumen and by being composed exclusively of glandular cells. Similar glandular cells can be found in *Jorunna tomentosa* and *Hypselodoris tricolor*, but not in this quantity nor thickness. Furthermore, in these species a lumen is always present. The family Phyllidiidae is sometimes united with the Dendrodorididae as *Porostomata* (Valdés 1996, Thollesson, 1998), but the oesophagus of *Phyllidia flava* differs in having no cells producing acid mucopolysaccharids. The cells in *Phyllidia* are elongate and only sparse, light blue tiny grana can be identified in the cytoplasm. No ciliated cells or special vacuolated cells were found in the oesophagus of *Dendrodoris nigra*. The thick layers of muscles around nearly the whole length of the oesophagus also seem to be unique. *Dendrodoris*, a sponge-eater, has no radula and it is assumed that the uptake of some food may occur by external digestion of the sponge-tissue before the actual sucking in of nutritive fluid takes place (Young 1969, Rudman 1998). According to our histological results, it seems probable that both the oral glands and the oesophagus secrete digestive enzymes. This secretion is expelled by contraction of the circular and longitudinal muscles surrounding the oesophagus. How far this musculature aids in sucking in the dissolved fluid, is not yet clear.

In the literature on *Dendrodoris*, the term "caecum" is used for a sac-like enlargement of the intestine just at the point where it bends to take a posteriorly directed course (e.g. Brodie et al. 1997). Since a caecum in Doridoidea is assumed to represent the (much reduced) right digestive gland (Schmekel & Portmann 1982, Wägele 1989), this term should not imply homology but is used in the literature as a functional term. In *Dendrodoris nigra*, this part of the intestine is not differentiated histologically in any way. A real caecum (homologous to the right digestive gland) could not be detected. Since the stomach is not demarcated from the digestive gland in most parts, it was not even possible to identify that part of the digestive gland which could represent the right part in ontogenesis. For several Atlantic *Dendrodoris* species, Valdés *et al.* (1996) described a bulb-like structure in this area, which they termed "pyloric gland",

but their interpretation was not based on histological investigations. We cannot confirm any glandular function for this area in *Dendrodoris nigra* and would prefer to use the neutral term "pyloric bulb" for this structure.

The genital tract of *Dendrodoris nigra* is of the typical triaulic type (Schmekel 1970). According to observations on gonad structures in several doridoidean species (unpublished results of senior author), a gonad intermingled with the digestive gland and kidney is apparently unique. But further examination of other taxa has to follow before its value for phylogenetic analyses can be discussed. From the contents of the receptaculum seminis and bursa copulatrix, we can conclude that all animals have mated at least once, although only the male stage was fully developed in the smallest animal and no oocytes were present in the gonad of this specimen. The entrance of the vestibular gland into the oviduct, next to its transition into the vestibulum is quite a long way away from the openings of vaginal duct and vas deferens. This gives the impression that the function of the vestibular gland has more to do with egg laying than receipt of sperm. The tall border of microvilli in the glandular epithelium of the vestibular gland in larger specimens is also very unusual. According to Brodie & Klussmann-Kolb (1998) they house many bacteria. Up to now, only a few species of *Dendrodoris* were known to possess a vestibular gland (e.g. *D. elongata*, Baba 1994, *D. goani* Rao & Kumary 1973). In our smallest specimen the vestibular gland was still lying within the notal tissue which suggests it might not have been visible when performing a dissection. In the light of this result, previous studies on smaller and lesser known species of the Dendrodorididae should be re-investigated.

In all three specimens examined, no cuticular structures were present at the penis. Penial spines are thought to be typical of mature *Dendrodoris nigra* (Kay & Young 1969, Edmunds 1971, Brodie *et al.* 1997), although this conclusion usually rests on only a few specimens. The absence of spines was also mentioned for only one specimen of *Dendrodoris fumata* by Brodie *et al.* (1997). They interpreted this as an artefact. It needs to be clarified, by a comparative analysis of many specimens, whether there exists a high intraspecific variability. On the basis of this, it must also be questioned as to whether the great emphasis Valdés *et al.* (1996) placed on the penial armature of *Dendrodoris* species as species-specific, is reasonable. According to their descriptions and figures, the differences in the spine structure of some of the species they dignose according to this character can also be interpreted as different stages in spine development.

Pericardial glands are present in the dorsal pericardial wall of *Dendrodoris nigra*, just as in some Doridoidea (including *Phyllidia*, unpublished results of senior author). Although these folds are called glands, their function as glands is not evident from the histological results.

There is no doubt that *Dendrodoris* belongs to the taxon Doridoidea since it shares all autapomorphies with this taxon (oesophagus without cuticular lining; triaulic genital system; blood gland next to, or on top of, cerebral ganglia; presence of gill glands; Wägele 1997). To clarify the phylogenetic relationship of the Dendrodorididae within the Doridoidea is more difficult, because an extensive analysis of the doridoidean families does not exist and many characters discussed here are not well known for other doridoideans. Usually

the Doridoidea are separated into two major groups, the Cryptobranchia and Phanerobranchia. This classification is partly based on the presence or absence of a gill cavity into which the gills can be retracted. Although Gosliner and Johnson (1994) consider the presence of a gill cavity as the apomorphic trait, it can also be observed in the phanerobranch family Onchidorididae. Considering the fact that protection of the gills might increase fitness, evolution of a gill cavity and the formation of muscles to retract the gills (or vice versa) could have occurred several times.

The possession of retractile gills, with a gill cavity and gill retractors, plus the general shape (oval, with notum larger than foot), and especially the tripinnate gills which are not observed in Onchidorididae support the hypothesis of *Dendrodoris* being a cryptobranch dorid. Nevertheless, the monophyly of the Cryptobranchia and Phanerobanchia still has to be clarified, and we need much more information on all other doridoidean families before the phylogenetic relationship of the Dendrodorididae can be solved.

Acknowledgements

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BOOK REVIEW

A revision of the Scaphopoda from Australian waters (Mollusca)
Kevin L. Lamprell & John M. Healy. 1998. *Records of the Australian Museum Supplement* **24:** 189 pp.

Like evolution, the process of naming the global molluscan fauna proceeds in leaps and bounds. And what a giant leap Kevin Lamprell and John Healy have made with the publication of their monograph on the Scaphopoda (tusk shells) of Australia. This comprehensive work, the first study of the countryís scaphopod fauna since 1959, covers all the 108 living Australian species, 47 of which are newly described, and 28 are named species not previously recorded from these waters. One new family (Omniglyptidae) is recorded and *Dentalium* (Dentaliidae), the largest genus in the work, contains 38 species. Each species has a full description of the shell and (where possible) the radula, each is compared with related species, and the distribution of each is summarised with a map. Australian fossil scaphopods are mentioned, but not reviewed taxonomically.

For me the most impressive aspect of this monograph lies in the great number of new species described. These 47 new species (43.5% of all the species in the monograph) reflect a totally unexpected biodiversity of the Scaphopoda in Australia. Many of these new species are presumed to be endemic. Prior to this work, Australian malacologists had relegated the Scaphopoda to the status of a `second class' class having very low diversity relative to the other major groups of molluscs (some 30 species were known). The statistics presented by Bouchet (1997) in his recent seminal paper `Inventorying the Molluscan Diversity' reinforce this impression. Bouchet showed that there had been an average of only 4.4 new fossil and living species of scaphopods described yearly in the world over the period 1967-1993. This figure compares with 657.8 for the Gastropoda. Obviously the Scaphopoda is much richer and more diverse than malacologists had previously believed, and Lamprell and Healy clearly indicate this Australian chapter is not the end of the story. They predict more new species and even new genera of scaphopods will be discovered in Australian waters when/if the collecting effort intensifies, particularly when additional sampling is undertaken in depths greater than 100 metres.

Another major taxonomic study of the Scaphopoda was undertaken simultaneously, yet independently, to the present study (Scarabino 1995). Victor Scarabino has documented the scaphopods collected on French expeditions in the tropical Indo-Pacific Ocean over the previous 20 years, many species coming from very deep water (800-3750 metres) and some of them from northern Australia. The most significant outcome in this context of unexpected biodiversity is the description by Scarabino of almost the same number of new species (42) as Lamprell and Healy. Clearly Pilsbry (in the preface to Pilsbry &

Sharp's (1897-1898) treatment of the Scaphopoda in the Manual of Conchology) was right when he exclaimed: `the list of species now known is doubtless a mere fraction of the grand total of living forms'. Little has changed after a century.

Lamprell and Healy's monograph stands significantly amongst others on Australian molluscs in that it was written by amateurs (i.e. `anyone who is not paid specifically for his/her work in malacology' following Bouchet's definition). Tragically this unexpected biodiversity would have gone unrecorded under the present strategic approach to research embraced by todays underfunded and understaffed scientific institutions. This work is a real tribute to the unstinting quest for knowledge for its own sake embodied by the endeavours of both authors.

In examining large series of specimens for most species, the authors have been able to assess intraspecific variation quite thoroughly. They concluded (page 6): `most conchological features vary to some extent within species but usually within definable limits.' The intraspecific variation they have documented is really more daunting than these words might indicate. For example, within a single population of *Dentalium exmouthensis* the apex varies from entire, to shallowly notched, to deeply notched, to deeply slit. As well, some anatomical features were discovered to vary significantly. For example the length of the radular ribbon varies between species and genera, and to some extent also between the sexes (females have relatively longer radulae than males of the same species).

This monograph's most attractive feature are the magnificent illustrations. All the species are illustrated by photographs as well as line drawings, each technique complimenting the other. The line drawings executed by Ms C. Eadie were prepared for *Mollusca: The Southern Synthesis* and demonstrate superb artistry in their own right

Lamprell and Healy's initial decisions in writing up this study will have a major impact on its longevity and utility. It is conchologically based and the authors make no pretence that the higher classification they have adopted will not change when anatomical data become available. Indeed they acknowledge (page 173) that there is already discord between shell-based and radular-based higher classifications and (page 174) that some species cannot be placed unequivocally into families on shell characters at present.

This tension between the demands of an objective taxonomy and the subjective assessment of characters is most obvious in the presentation of dichotomous keys utilising only shell characters. The inclusion of such keys as an aid to naming species is highly commendable, but constructing robust keys is an extremely difficult task. In constructing a key, one must assume the reader has no knowledge of either the subject or the authors' preconceptions. In other words, there must be no possibility for subjective assessment of characters on the part of the reader. In my opinion some of the alternatives in the keys in the work are overly simplistic because of the *a priori* assumption the reader has the same knowledge base as the authors and this is not always the case. For instance I went wrong in using the key to families of the Dentaliida (page 15) to identify a common species from the Darwin area. I could clearly make out microscopic longitudinal ornamentation on the apical section of all the shells before me so I

concluded the species belonged to Dentaliidae. In fact it belongs to the Laevidentaliidae which should have completely smooth shells according to the first dichotomy in the key. How was I to know that there was a subjective difference between the magnitude of the ornamentation; strong ribs (Dentaliidae) versus weak striae (all other families)? In fact the longitudinal ornamentation on the shell of the species I was keying out (*Laevidentalium longitorsum*) is very similar to that of species of *Grapacme* (Dentaliidae), so I did not feel so disappointed when I eventually found out (page 127) that the placement of *L. longitorsum* in the Laevidentaliidae is not settled. Neither, it seems, is the family for the oldest fossil species assigned to the Scaphopoda established conclusively for exactly the same reason; *Rhytidentalium kentuckyense* dates from the Middle Ordovician of North America. It appears to have a smooth shell and so was originally placed in the Laevidentaliidae, but Lamprell and Healy question this placement (page 11) because they argue any weak longitudinal ornamentation that could have been present on the shell would have been lost through the process of fossilisation. Could they tacitly doubt the importance of longitudinal ornamentation as a character in scaphopod taxonomy themselves?

As long as readers heed the cautions that Lamprell and Healy have stressed in their descriptions and in the foreword to their keys - about not attempting to identify single, eroded, or juvenile shells - the majority of the keys work very well. After giving this monograph a thorough `road test' with the scaphopod collection in the Museum and Art Gallery of the Northern Territory I am convinced the work is vastly better for the inclusion of keys than it would have been without them.

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BOOK REVIEW

Indo-West Pacific Ranellidae, Bursidae and Personidae (Mollusca:Gastropoda). A monograph of the New Caledonian fauna and revisions of related taxa.
Alan G. Beu
Mèmoires du Muséum National d'Histoire Naturelle, **vol. 178.** (*Résultats des Campagnes MUSORSTOM,* **vol. 19**). pp. 255. (22 by 28 cm, hardbound).

Order from Universal Book Services, PO Box 321, NL-2300 AH Leiden, The Netherlands.
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For more than a decade since 1984, two French institutions, the Muséum National d'Histoire Naturelle and ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Cooperation), have conducted a joint research programme in the seas around New Caledonia. In all, more than a dozen MUSORSTOM expeditions and cruises have surveyed the lagoons and shallow reefs of New Caledonia, and an area of deep water from the Coral Sea to southern Vanuatu. This ambitious sampling programme has resulted in an enormous quantity of marine collections, which are reported upon in the continuing series of the Résultats des Campagnes MUSORSTOM, of which the present volume is number 19. Two previous volumes (7 and 14) have also dealt specifically with molluscs, and other molluscan papers have appeared in the series, but this is the first volume to be entirely devoted to a single closely related group of molluscs, the families Ranellidae, Bursidae and Personidae. This scholarly work is the culmination of 20 years of research by Dr Alan Beu, and is therefore the result of the study of a remarkable collection of material by the foremost authority on these tonnoidean families.

Previously, only 28 species had been recorded in the New Caledonian fauna. This was an entirely inadequate total, for even the shallow-water sampling of lagoons and reefs during the MUSORSTOM expeditions and by local divers produced an additional 20 species. Among these is a new endemic *Distorsio* and several species of these families not previously reported from south of the equator. Also surprising are the new records of four species previously considered to have Australasian distributions in the southwestern Pacific (*Charonia lampas, Cymatium exaratum, C. parthenopeum, C. dunkeri*). The discoveries in deeper water are still more remarkable, and have revealed a diverse new tonnoidean fauna dominated by abundant *Sassia remensa* (hitherto considered Australasian), *Bursa fijiensis* (not reported since the 'Challenger' Expedition), *B. latitudo* and *Distorsio habei*. Among the diverse small personids from this deep-water material are two new species which are the first recorded living members of *Personopsis*, a genus hitherto limited to fossils from the Palaeocene to Pliocene. These discoveries bring the fauna of the New

Caledonian region to 73 species. To put this diversity in perspective, Beu gives a critical list of the entire tropical Indo-West Pacific fauna of these three tonnoidean families, which numbers 145 species and subspecies.

This is essentially a taxonomic and nomenclatural work. However, it is more than simply an account of the species from the vicinity of New Caledonia. Where difficult taxonomic problems required it, Beu has included revisions of extra-limital species. Thus the volume includes complete monographic revisions of *Biplex, Gyrineum, Cymatium (Gelagna)* and the southwestern Pacific species of *Sassia,* besides accounts of a number of *Cymatium* and *Distorsio* species related to those in the New Caledonian material. Of the seven new species proposed, three are from outside the region. The book is superbly produced, with a hard coloured cover, four colour plates and numerous good halftones (including SEM details of protoconchs and sculpture). For each species there is a detailed synonymy and thorough discussion of types. In order to stabilize the nomenclature, some 88 lectotypes and neotypes are established. Of wider interest to molluscan taxonomists are the introductory notes on the fate and whereabouts of some significant historical collections, including that of Gualtieri (in the University of Pisa) and the Japanese material of Lischke (Löbbecke Museum, Düsseldorf). With the exception of the new taxa, no space is wasted on descriptions; instead, reliance is placed on the figures and discussion of distinguishing features and related taxa. Although the MUSORSTOM station numbers are listed exhaustively, together with much additional material examined, there are unfortunately only two distribution maps; perhaps it was felt that distributions of these tonnoideans are as yet too incompletely known for mapping. Fossil occurrences and some exclusively fossil species are also included. It has to be said that this is a taxonomy based almost entirely on shells, albeit on an admirable range of material. Anatomical remarks are limited to occasional comments on animal coloration, some generic characters of radulae, and family-level traits (the third accessory salivary gland of Bursidae, for example). Not a single radula is illustrated, not even for the two new genera proposed, nor for the first living *Personopsis*. It is indeed the regrettable case that much of the unique molluscan material from the MUSORSTOM expeditions is dry, so that important anatomical and dietary information has been lost, yet it must be supposed that animals could be reconstituted and, at the very least, radulae prepared.

One well known biological feature of these families is that many members possess long-lived, and hence widely-dispersed, teleplanic larvae. This makes the biogeography of the tonnoideans especially interesting. Many have very wide distributions, which may explain why only four of the species from the New Caledonian region were undescribed. This study has expanded the known range of numerous species, showing for example that the apparent restriction of many to the Philippines is simply an artefact of inadequate sampling elsewhere. Indeed, based on the data for this group the classical focus of Indo-West Pacific diversity in the Philippines and Indonesia can be extended to include New Caledonia. Among the taxa with the very widest distributions are *Charonia lampas* and *Cymatium parthenopeum,* both found in the northern and southern temperate fringes of the Pacific (and also in the Atlantic); Beu makes the

interesting suggestion that these are unable to compete with ecologically similar tropical taxa (*Charonia tritonis* and *Cymatium pileare* respectively), but that the occasional records in New Caledonia suggest the possibility of genetic exchange between parts of the distributions formerly considered to represent isolated geographical subspecies.

These geographically widespread, polytypic species illustrate just one of the problems of relying solely on shells for classification. While the shallow-water material of *Charonia lampas* from the Pacific fringes appears to fall into recognizable geographical forms, specimens from deeper water are all pale and weakly sculptured, which Beu interprets as ecophenotypic variation. From this, he argues against the recognition of geographical subspecies in this case. However, elsewhere (as in the newly described *Biplex bozzettii*) very subtle differences in shell shape and ornamentation are used to discriminate species, even when these are not sympatric, so that clinal variation cannot be ruled out. In other cases disjunct distributions are accepted despite slight geographical differentiation; an example is *Cymatium dunkeri*, although here there is some inconsistancy, for in the Introduction the southern Pacific form is named *C. iredalei*. Even at the generic level, shell characters can prove unsatisfactory. As Beu admits in his discussions of the large genera *Cymatium* and *Bursa*, supraspecific classification is `a question of whether imprecise, intergrading characters can be used at the generic level' (p. 143). This volume has done an admirable job in stabilising historical nomenclature and setting out a primary taxonomy. From this important foundation the systematics of the tonnoideans must now be moved forward. It is time to look for new characters with which to test the ideas on species concepts and phylogenetic relationships that Beu has outlined.

This is a book that can only be recommended for the most dedicated specialist and for institutional libraries. Many of the illustrated species are deep-water forms unlikely to be encountered by researchers, divers or collectors. Despite the biogeographic interest of these families, there is hardly any discussion of the distributional data presented for a wider audience. Apart from precise depth ranges, there is almost no ecological information about habitat, species associations or diets. Even for the specialist malacological community this book cannot be used as a primary source of information on the classification of the Ranellidae, Bursidae and Personidae, since coverage of species beyond New Caledonia is sporadic, and in many cases the supraspecific taxa are not formally defined. Some readers will not be familiar with the family Personidae, for example; indeed, Beu himself only recognized this group in 1988, yet there is no discussion or definition of this family to be found here. Nevertheless, this is a landmark among studies of the Tonnoidea, and will be the first place of reference for identification of Indo-West Pacific species.

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MOLLUSCAN RESEARCH

Volume 20, Number 1 16 June 1999

CONTENTS

A.V. Korniushin & N. Glushchenko
Anatomy of New Zealand species of the family Sphaeriidae (Bivalvia, Eulamellibranchia) 1

B. J. Kefford & P. S. Lake
Effects of spatial and temporal changes in water velocity on the density of the freshwater snail *Potamopyrgus antipodarum* (Gray) 11

W. F. Ponder
Calopia (Calopiidae), a new genus and family of estuarine gastropods (Caenogastropoda: Rissooidea) from Australia 17

I.T. Hyman
A comparison of two onchidiid species (Mollusca, Pulmonata) 61

K.L. Lamprell & J.M. Healy
Granicorium from Australian waters, with descriptions of a new species (Mollusca: Bivalvia: Veneridae) 73

H. Wägele, G.D. Brodie & A. Klussmann-Kolb
Histological investigations on *Dendrodoris nigra* (Stimpson, 1855) (Gastropoda, Nudibranchia, Dendrodoridídae) 79

Book Review
R. Willan
A revision of the Scaphopoda from Australian waters by K.L. Lamprell & J.M. Healy. 95

David G. Reid
Indo-West Pacific Ranellidae, Bursidae and Personidae (Mollusca:Gastropoda). A monograph of the New Caledonian fauna and revisions of related taxa by A.G. Beu 98